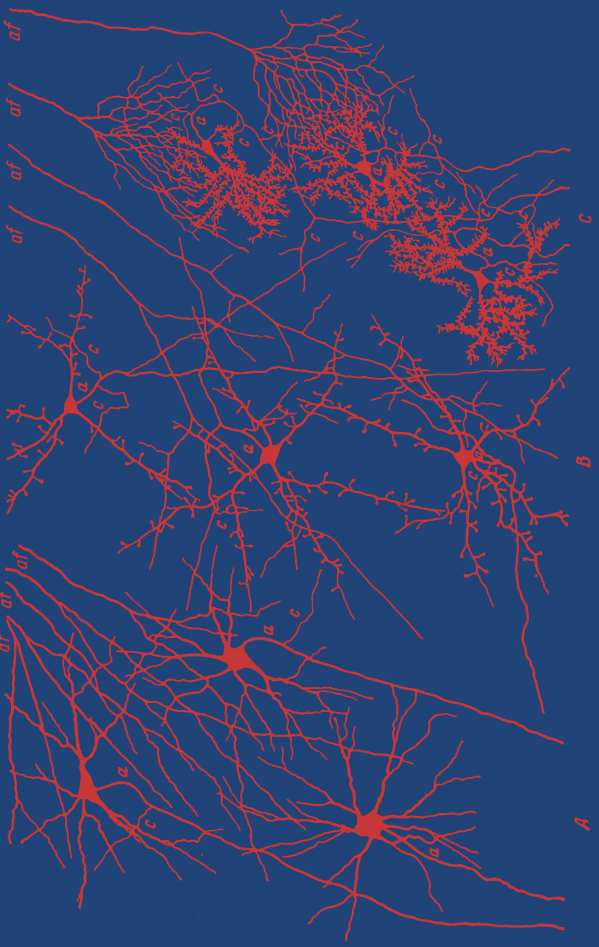
G. I. POLIAKOV

ON THE NEURONAL ORGANIZATION OF THE BRAIN



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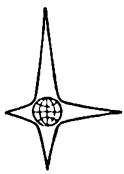

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Г. И. ПОЛЯКОВ

О ПРИНЦИПАХ НЕЙРОННОЙ ОРГАНИЗАЦИИ МОЗГА

ИЗДАТЕЛЬСТВО
МОСКОВСКОГО УНИВЕРСИТЕТА

ON THE NEURONAL ORGANIZATION OF THE BRAIN

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INTRODUCTION

This monograph is devoted to a description of certain processes relating to the establishment, development, complication, and perfection of the organization of reflex mechanisms in the evolution of animal organisms.

The construction of the brain as an organ of reflex reflection of the environment and organizer of behaviour is more and more occupying the attention of investigators, and is the object of intensive experimental study The future progress of our knowledge in this field undoubtedly depends on systematic accumulation of factual data revealing ever newer details of the finest (microscopic and ultramicroscopic) structures of the brain matter and of the connections between its separate constituent elements.

As our factual material increases in volume so too our need to understand it grows. In the present work we have endeavoured to generalize the data available on the anatomy, physiology, and evolution of the nervous system, taking into account the most recent advances in the field of modelling certain properties of physiological systems. One can only speak at present, of course, of hypotheses providing an explanation of the general plan of the brain's structure. The parallels drawn between natural and technical systems, it should be noted, are predominantly limited to the simplest models of a reflex arc or of a separate neuron. When it is a matter of the more complex mechanisms of the brain (for example, in making models of conditioned reflexes), concrete analysis is usually replaced by general schemes and to that extent the real complexity of their structure as a whole is not reflected. Despite the undoubted efficacy of that kind of approach on the purely cybernetic plane, the neuromorphologist cannot overlook the fact that

there is 'too much cybernetics' in these attempts and too little real knowledge of the brain.

Chapter I reviews the round of problems relating to the ground plan of the organization of various reflex mechanisms that differ in level of development and are formed in a definite sequence during the evolution of the animal kingdom. It is important in this connection to stress that we have taken as the basis of our analysis of the construction of the brain not its generally accepted division into anatomical parts but the new principle of functional localization, which is surveyed in detail in Chapter II.

In tracing the various stages of the complication of animal reactions (together with their corresponding transformations of neuronal structure) from the standpoint of their evolution, we consider them as the material expression of the interaction of three main functions governing the whole adaptive potential of the organism, namely the functions of regulation, control, and direction in their broad sense, that is to say, including auto-regulation, auto-control and auto-direction.*

In our conception these functions and their morphological substrata are the neurophysiological foundation for active orientation in the external world, analysis and synthesis of all extrinsic and intrinsic signalling, and the programming and performance of responses to stimulation. These functions, we suggest, embrace all manifestations of reflex activity from the simplest to the most complex at all stages of evolutionary development. As will be shown later, it is possible to distinguish a reflex mechanism for each of these functions, a mechanism clearly delineated spatially (topographically) and linked to corresponding complexes of neurons and their interconnections.

In order to avoid misunderstanding we deem it necessary to make the following reservation. We have not found in the specialist literature any clear definition of what

---

* In our article 'Problems of Regulation, Control, and Direction from the Neurophysiological Aspect' (in *Problemy kibernetiki*, No. 11, Moscow, 1964), we used the following terms: self-regulation and regulation, self-control and control, and self-direction and direction. In the present work we have decided to use 'auto' instead of 'self' in order to distinguish our definitions of these terms more clearly from the interpretation generally given to them in psychological literature.

should be understood by the terms 'regulation', 'control', and 'direction' In our understanding of these functions we have been guided exclusively by the logic of the analysis of the reflex arrangements of biological objects (animal organisms). We consider them to be governed on the neurophysiological plane by the laws of self-organizing natural systems.

We must also emphasize the following proposition. We consider the function of direction (together with the more complex forms of analytical and synthesizing treatment of all information received by the organism) as the highest phenomenon of reflex activity (higher nervous activity in Pavlov's terminology). We link this function with the most highly organized divisions of the central nervous system, and those of regulation and control (as we define them) with the lower levels of the analysers, considering them only as supplementary to the main function of direction (which acquires the quality of the true organizer of the whole strategy and tactics of behaviour). Our definitions of 'regulation' and 'control' differ from those generally used and have a different meaning. The phenomena of higher nervous activity in man, which are often treated on the psychological plane as regulation and control, from our point of view are various forms of expression of the one all-embracing function in man, direction. In that respect we are inclined to agree with those members of the cybernetic trend who prefer to speak only of a function of direction in defining the tasks of their field.

Chapters III and IV are devoted to the principles of the origin of the neuronal network and to the general scheme of organization of neuronal switches in the central nervous system. In our view one common principle of universal significance for the whole animal kingdom underlies the building of all nervous systems from the simplest to the most complex. Any neuron, as the elementary unit of a switching apparatus, is (in relation to this principle) a point of convergence and divergence of the impulses switched in it, i.e. is an instrument performing a definite form of analysis, synthesis, and selection (filtration) at the nerve-cell level of signals passing through it. This pattern, which is asserted at all stages of evolution and at all levels of the nervous system, enables us to outline a general scheme of the consecutive complication of the organization of neuro-

nal switches, beginning at the primitive nerve network of lower multicellular creatures and ending with the most complexly organized brain of the higher vertebrates and man.

In particular, taking this universal structural feature as our starting point, we discuss the problem of a rational classification of the division of the cerebral cortex into its functionally different areas (architectonic regions and fields). The classification of cortical formations that we propose here is also based on the very rich experience of years of clinical observation of cortical lesions.

The propositions that we advance in this work are only, of course, working hypotheses and are open to discussion. But first hand acquaintance with them could be of interest to a wide circle of specialists—psychologists, teachers, biologists, physicists, and all those who are working on the building of experimental models of biological systems, as well as neurologists (neuro-anatomists, neurophysiologists, and clinicians).

We feel that the material presented here can be of some measure of assistance to philosophical understanding of the structure of the brain as an organ of reflection (modelling) of objective reality in the consciousness of the perceiving subject. From that point of view in particular we would draw attention to the mechanisms of closed circulation of impulses and of mutual excitation of neurons discussed by us in Chapter IV as the anatomical and physiological basis for the accumulation and imprinting of information in the cortex. The related processes we qualify as the material basis of the reflex movement of the organism in space and time. It seems to us that there are great perspectives here for philosophical consideration of our representation of the general plan of the various levels of switching apparatus in the brain as consecutive stages in a transition from more concrete forms of perception of reality to more and more abstract forms of cognizing it linked with a capacity to operate with abstract categories (processes of generalization and abstraction).

The material outlined in our present work is, of course, only a fragment of the future theory of the neuronal organization of the brain.

CHAPTER I

REFLEX MECHANISMS OF THE BRAIN

Organs of Signalling Activity

The nervous system has developed in the evolution of the animal kingdom as an organ providing the most perfected form of adaptation to the conditions of the environment by means of signalling activity. Unlike plants, which react with changes of biological activity only to direct external influences, animals are capable of reacting to the signal significance of stimuli. That means that an animal perceives a stimulus not only as a direct physical or chemical effect on its organism but also as a signal or warning of the approach of definite events important to its life. Consequently animals differ from plants in their ability to apprehend the information contained in signals that is of essential importance to the organism, and to rework it into responsive actions.

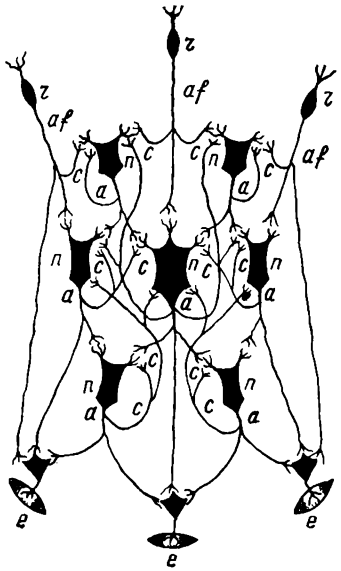
The material substratum of the signal function consists of three basic elements articulated in a definite sequence along the pathway of a reflex arc, as follows (see Fig. 1):

receptors — the cells of the sense organ, which perceive stimuli and transform them into nerve impulses;

neurons — nerve cells and their processes, which effect the various switchings of nerve impulses on the pathway from the original link of the reflex arc to the final one;

effectors — the cells of muscles and glands, elements by which the reflex response of the organism to stimulation is realized.

The basic structural units of the nervous system, neurons, have originated and developed during the evolution of the animal kingdom as a special apparatus linking receptors and effectors; and it is they that are responsible for interpreting the signal significance of stimuli and elaborating biologically useful, adaptive reactions.



F i g. 1. Diagram of a differentiated network of neurons; *r*, receptors; *af*, peripheral sensory (afferent) fibres conveying impulses from receptors to neurons; *n*, neurons; *a*, the nerve fibres (axons) of nerve cells, with their collateral branchings (*c*) contacting the bodies of other nerve cells and their dendrite branchings; *e*, effectors.

The elements of the reflex arc are articulated by means of special formations, synapses, which will be considered in greater detail in Chapter III. The successive transmission of impulses triggered by the action of stimuli first from receptors to neurons, then from one group of neurons to another, and finally from neurons to effectors, occurs across synapses.

As relations with the external world became more complex during the development of the animal kingdom, the mechanisms of reflex (signalling) activity grew extraordinarily complicated. In their elementary forms they are a network of neurons (Fig. 1) consisting of combinations of receptors, neurons, and effectors that are still relatively simple and first arise in the lower multicellular organisms (Coelenterata). Such an organization of the nervous system, from which its progressive differentiation has developed,

already possesses the property of effecting a coordinated, i.e. ordered and biologically expedient, reflex response to stimulation.

The further complication of the apparatuses for receiving signals and responding to them consists in the following developments. The nervous mechanism of coordinated reflex activity developing at the earlier stages of evolution is only able to effect an ordered response to relatively few combinations of signals of vital significance to the self-preservation and continuation of the species. But this mechanism is clearly insufficient when the organism needs to orient itself to more complex combinations of signal stimuli. By themselves these stimuli cannot threaten its integrity, and do not come directly from food; they signal only various changes in the ambient situation.

On the next rungs of the evolutionary ladder the organism can not only respond to a definite complex of stimuli with immediate coordinated reflex activities but is also able to reflect the spatial and temporal connections between objects and phenomena in a more complicated and indirect way in its reactions. So a more differentiated orientation is achieved among the objects of the external world and their interrelations.

Thus there is a transition from elementary, sensory reflection of the quality and intensity of stimuli to reflection of the images of things and phenomena, i.e. to the reproduction of more complicated brain models, a process that corresponds to a higher stage of development of the signalling system or, as Pavlov called it, of higher nervous activity.

Figuratively speaking, animals with an as yet weakly developed signalling activity, which are capable of an ordered reaction only to a relatively narrow round of stimuli, may be likened to a kind of living, self-adapting, reflex, 'automaton' Organisms that react to a wider range of stimuli, and posses higher forms of reflecting reality, have to process a considerably larger volume of information about their surroundings. In comparison with lower creatures that have to do with a minimum of information these organisms possess 'surplus' information as it were and are able to select the optimum solution from many possibilities, i.e. they can 'weigh up' or 'solve' logical problems. The development of just that property leads at the highest

stages of the animal kingdom to the appearance of thinking beings.

As recepts become more complicated so, too, does the character of the responses. In the complex fusion of conditioned and unconditioned reflexes from which animal behaviour is built up, new forms of motor coordination developed during its lifetime begin more and more to predominate.

These transformations in the character of the functional relations of the organism with its environment could not avoid being reflected, of course, in the structural organization of the sense organs and nervous system, which found expression in the development of analysers.

The complex sets of neurons that make up analysers are the material basis for a whole variety of functional links between separate signals and combinations of signals, so determining the character of the relations between stimuli, and on that basis elaborating a programme of responses.

Analysers developed in the course of evolution as the most highly organized part of the neuronal structure of the animal brain, with the fundamental biological purpose of breaking down individual signal stimuli and exciting reactions to definite complexes and interrelations of stimuli. Analysers, as Pavlov pointed out, are developed instruments for fine analysis and broad synthesis of stimuli.

Among the highest vertebrates the complex chains of neuron switches, from which the analyser systems are built up, are located at various levels of the central nervous system (see Fig. 7) and adapted to completing the circuit of the various components of the reflex reactions which in their aggregate constitute integrated behaviour. The analyser systems that permeate the whole central nervous system are the most important part of the substratum of the brain, which brings about a physiological unity of conditioned and unconditioned reflexes and so ensures adequate adaptation to the environment.

It is not without interest that the evolved complication of the organism's material apparatus of signalling activity coincides in certain respects with the ideas of Mackay (1956). It is possible to draw certain parallels between the coordination mechanism and analysers on the one

hand (see below), and the lower and higher forms of automata on the other. The lower forms (automata of the first order) work on the scheme automaton-medium. They can only carry out the elementary function of direct 'recoding' of signals received from outside. Higher forms (automata of the second order) have a built-in mechanism for comparing external signalization with their own programmes of behaviour; the mechanism is in a position to reproduce copies, or models, of certain special factors of the objects and phenomena acting on the automaton and thus performs the function of an analogue of the environment. As will be seen in the next section, an essential distinction between the coordination mechanism and the analysers is that the latter provide the organism with a fuller and more all-round orientation in its surroundings.

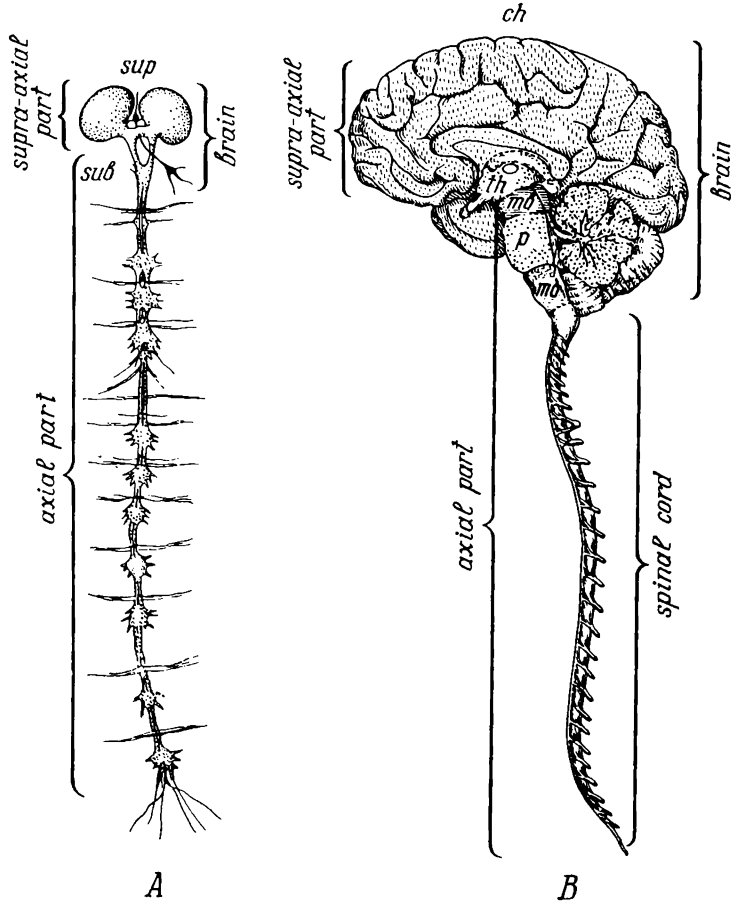
2. Basic Divisions of the Nervous System

In this section we shall consider the general plan of the reflex mechanisms of the brain at various levels of complexity, and in the next chapter the relation of these mechanisms to the basic nervous functions of regulation, control, and direction.

In the evolution of animal organisms possessing nervous system, as we have already said, a mechanism first begins to take shape that is able to provide a coordinated reflex response to stimulation. In other words the elementary network of neurons (Fig. 1) represents above all a **coordination mechanism.**

This organization becomes clearly differentiated in the earliest phases of evolution. Thus the simplest unicellular creatures, possessing only the rudiments of sense organs and a nervous system, are capable of performing ordered reactions, i.e. of producing a selection of definite reflexes biologically most expedient in the situation, and of inhibiting reflexes that hamper the carrying out of this activity.

As evolution proceeded the mechanism of coordinated responses to stimulations naturally became extraordinarily complex and specialized. Nevertheless, in all members of the animal kingdom, whether invertebrate or vertebrate, from the lowest to the highest, special groups of neurons can be distinguished that are responsible for this side of reflex activity.



F i g. 2. *A*, centralized ganglial nervous system of higher invertebrates (insects); *sup*, supraglottal head ganglia; *sub*, subglottal head ganglia; *B*, vertebrate central nervous system (human brain); *ch*, cerebral hemispheres; *th*, thalamus (between-brain); *mb*, mid-brain (corpora quadrigemina and cerebral peduncles); *p*, pons; *mo*, medulla oblongata.

In animals with bilaterally symmetric bodies (beginning with the worms) the coordination mechanism is the cord or axis of their centralized nervous system (Fig. 2). In invertebrates it corresponds to the trunk ganglia (Fig. 2 *A*),

i.e. to the nerve cord in the lower worms, to the chain of ganglia in the segmented worms, crustaceans, arachnida, and insects. At these stages of evolution, the chain of ganglia located along the trunk has, it would seem, a reflex function analogous to the activity of the coordination mechanism in vertebrates.

In vertebrates this mechanism is located along the whole axis of the central nervous system (spinal cord and brain-stem—see Fig. 2*B*), occupying its central portions.* It is important to note here the relatively immediate character of the connections between the receptors, neurons, and effectors making up the coordination mechanism; it may be taken that there are only as many of these elements as are necessary to provide certain coordinated reflex, and no more.

A qualitative complication of this arrangement, in connection with the extension of the organism's orientation in the world around it and the far-reaching transformations of the whole sphere of its recepts and activity, is the development of **analysers.** The physiological significance of the evolution of these sections of the whole reflex apparatus is that they enable the organism to differentiate among the host of 'side' stimuli apart from those directly processed by the coordination mechanism, and ensure the adaptation to the environment vital to its existence. Thanks to the development of analysers the organism receives a mass of supplementary 'input' and 'output' at the periphery of its body facing the outside world. It is thus in a position to react selectively to a variety of signals of a significance far beyond what is required for the direct security of a living system.

Pavlov conceived the analysers, of course, as complex chains for switching nerve impulses beginning on some sense organ or other and ending in the brain. Accordingly he distinguished between the peripheral and the central cerebral end of every analyser. In the more highly organized members of the animal kingdom the highest, cerebral end of an analyser system lies in a definite region of the cortex of the cerebral hemispheres (see Fig. 7).

The essential distinction between the cerebral and periph-

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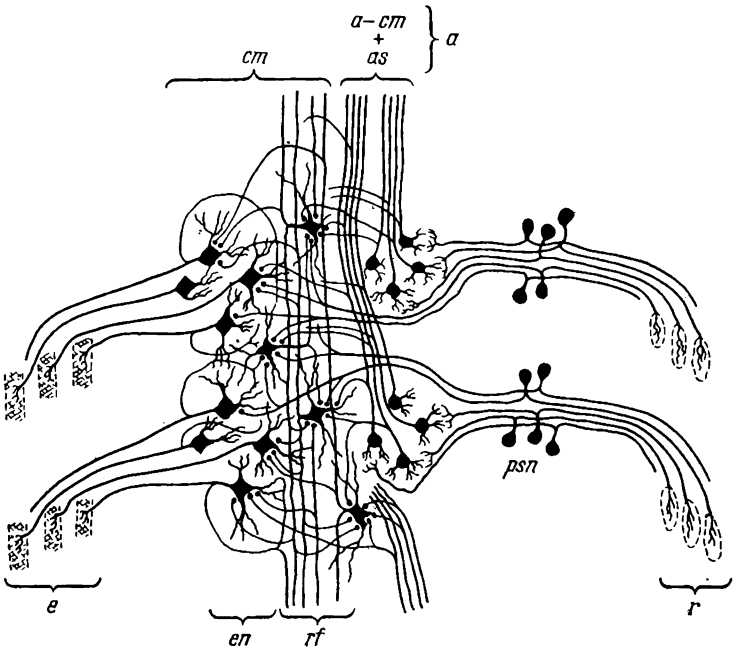
* Hereafter the central nervous system will be referred to as the CNS.



F i g. 3. Diagram of the switching devices in the CNS forming the coordination mechanism (*cm*) and analysers (*a*). The latter include the analyser-coordination mechanism (*a-cm*) and the analyser systems (*as*); *r*, receptors; *psn*, peripheral sensory neurons, lying in the ganglia of the spinal and cranial nerves; *rf*, internuncial neurons of the coordination mechanism (reticular formation); *en*, effector (motor) neurons innervating effectors; *e*, effectors (skeletal muscles).

eral parts of an analyser is as follows. The receptor elements of the sensory organs and the peripheral sensory neurons directly connected with them (see Fig. 3, *psn*) are adapted exclusively to purely 'mechanical' discrimination between stimuli according to their physical qualities (frequency, intensity, duration, etc.). The cerebral parts of the analysers are specialized for central processes of analysis and synthesis of stimuli, not simply according to their physical and chemical parameters but also, and mainly, according to their signal significance for the life

of the organism. Only on the basis of such indirect processing of nerve signals are the programmes or formulae of the organism's responses and actions worked out. We take as cerebral parts of the analysers only those groups of central switching neurons and their interconnections that can be regarded as a supplementary superstructure on those of the coordination mechanism proper (Fig. 3; see also Fig. 19). In the centralized nervous system the analysers are the assemblages of neurons formed initially at the 'entries' to the neuronal network, i.e. at the points where impulses from the peripheral sensory neurons are transferred to the coordination mechanism. The analysers are a supplementary switching apparatus inserted between the whole receptive sphere of the organism and the apparatus that directly organizes its coordinated responses to stimulation.

From these topographical, anatomical relations it follows that the basic physiological and biological purpose of analysers is precisely to organize the organism's whole receptive sphere. In their cerebral parts an interaction takes place between the various centripetal impulses being received from the sense organs and takes place even before the appropriate signals, transformed in a definite way, are passed to the coordination mechanism and transformed in it into some sort of final effector activity.

At bottom the coordination mechanism is concerned with processing relatively simple combinations of biologically adequate stimuli that have not yet been combined in a more complex physiological synthesis. The activity of the cerebral parts of the analysers provides the most highly organized central coordinations within the receptive sphere itself, i.e. an ordered analysis and synthesis in both space and time of complexes of stimuli united into definite systems of interrelations thanks to which the organism as a complexly differentiated whole acquires the possibility of orienting itself and operating in the external world.

A vivid example of the kind of coordination elaborated in the receptive sphere is Stratton's famous experiment (1897) with glasses furnished with lenses that gave an inverted image. Within a few days subjects fully recovered visual orientation in the space around them, and their normal perception of objects was restored.

All the reflex responses of animals that possess developed analysers are refracted as it were through the prism

of the processes of analysis and synthesis of stimuli that take place in them.

The functional possibilities built into the coordination mechanism proper are very limited in the sphere of the organism's interrelations with its environment. The mechanism is a reflex apparatus only suitable for performing separate, more or less elementary, accommodations in a relatively narrow area of life. Analysers considerably extend the boundaries of the organism's adaptive possibilities.

The reactions completed through the coordination mechanism to some extent have a 'fleeting' character instantaneously correlating the physical parameters of stimuli (their strength, duration, frequency, etc.) with the physiological parameters of relatively simple reflex arcs.

The functional possibilities of the cerebral parts of the analysers are considerably broader than those of the coordination mechanism; and thanks to their more complex neuronal organization they have the conditions needed not only to synthesize the various reactions, being performed at any moment but also to link them functionally in time. In other words, not only is the character of the operating stimuli correlated there directly and instantaneously with that of the effector responses to them but there is also a complex indirect relating of the activity taking place at a given moment with the results of reflex acts previously completed.

Analysers are obviously a more developed tool for reflex reflection of the environment as a complex, interrelated whole through which the organism is able to adapt itself to ever more varied combinations of stimuli. With their development there first arose in the animal kingdom a differentiated material foundation on which was built a succession of individual experiences; and *pari passu* the organism's potential 'foreseeing' the probable consequences of its actions increased. In the cerebral parts of the analysers, as will be shown later, special formations developed, organized on the cortical type (see Plate I) and specially adapted to perform the most complex reflex functions.

The development of analysers was brought about by a qualitative complication of the reactions relating the organism to the external world; and in their progressive

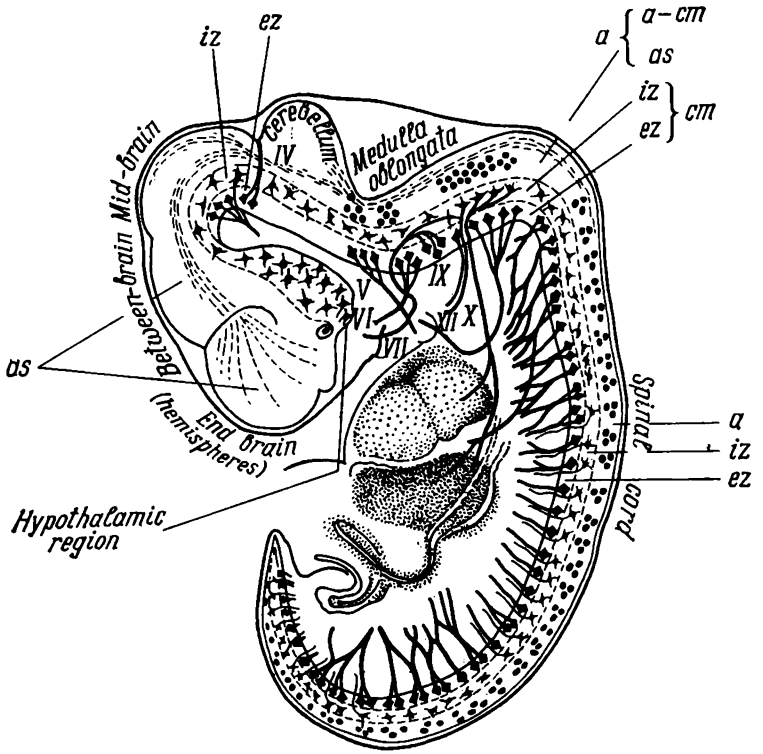
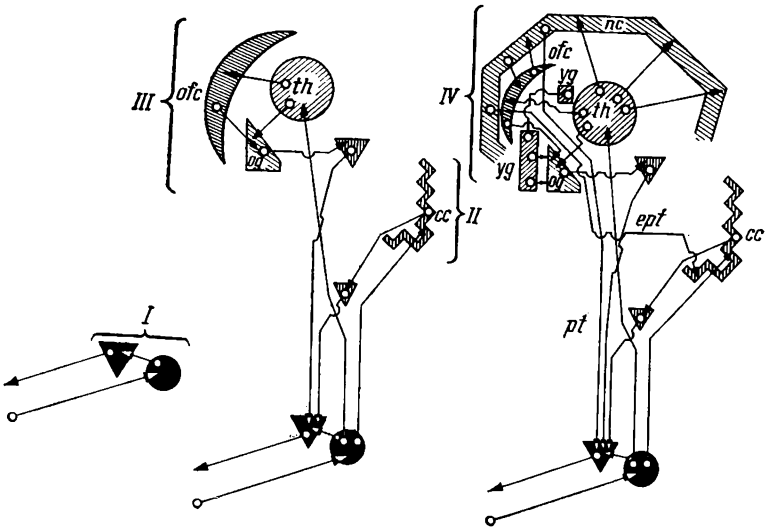


Fig. 4. Schematic picture of the basic divisions of the CNS of vertebrates (the human foetus in the early stages of its development). Roman numerals indicate the motor portions of the corresponding cranial nerves; *ez*, zone of effector (motor) neurons and their processes to the periphery; *iz*, zone of internuncial neurons of the axial part of the CNS (reticular formation); *iz*+*ez* constitute the coordination mechanism (*cm*); *a*, zone of analysers, from which the analyser-coordination mechanism (*a-cm*) and analyser systems (*as*) are differentiated during subsequent development. It can be seen that the reticular formation also extends to the supra-axial part of the CNS (see the hypothalamic region of the between-brain). The higher sections of the CNS, the hemispheres of the end-brain, develop completely from zone of analysers. (In part after His, supplemented by the latest research of Zhukova and Leontovich.)

development it was the influence of the external medium of the organism, rather than the internal, that was the essential factor.



F i g. 5. Diagram of the evolutionary 'overgrowth' of the coordination mechanism by analyser formations; *cc*, cerebellar cortex; *th*, thalamus; *ofc*, complex of the phylogenetically older formations of the cortex (palaeo-archicortex); *og*, phylogenetically older part of the subcortical ganglia of the cerebral hemispheres; *yg*, phylogenetically younger part of the subcortical ganglia; *nc*, formations of the fully developed cerebral cortex (neocortex) appearing last in the evolution of vertebrates; *pt*, pyramidal tract conducting impulses of voluntary movement arising in the cerebral cortex to the reflex centres of the coordinating mechanism; *ept*, extrapyramidal tract conducting influences of the cerebral cortex to the cerebellar cortex. The lower reflex centres of brain-stem and spinal cord are represented by black triangles and circles. *I*, corresponds to the coordination mechanism; *II* is the analyser-coordination mechanism; *III* and *IV* correspond to two successive stages in the progressive complication of the higher (supra-axial) ends of the analyser systems (after Bernstein, with modifications).

In a rudimentary and still, as it were, undeveloped form, analysers arose in the more highly developed invertebrates with central representation in the brain (the supraglottal ganglia in worms, insects, and crustaceans) (see Fig. 2*A*); but only in vertebrates do they enter the decisive phase of their development, taking up ever greater sectors of the central and peripheral nervous systems (Fig. 4). The chains of neuron switches from which they are built up are super-

imposed on the assemblage of neurons that constitutes the coordination mechanism (see Fig. 7). Dominating the latter to an ever greater degree, the analysers utilize the possibilities it contains for more effective and flexible adaptation of the organism to a variety of changing situations; and with their 'progressive development the coordination mechanism is more and more subordinated to them, becoming their obedient instrument fulfilling commands received from them. In the course of evolution the coordination mechanism, which occupies a pivotal position, is more and more overgrown by analyser formations (Fig. 5), and the latter, though having developed from it, at the same time gradually become emancipated from it.

Thus the centralized nervous system* can be pictured at definite stages of evolution as a coordination mechanism plus an aggregate of complexly interconnected cerebral parts of the analysers. Progressive increase in the absolute and relative number of central switching neurons in the analysers in relation to the number of neurons in the coordination mechanism can therefore be taken as an objective criterion of a higher level of neuronal organization. From the standpoint of comparative evolution we can distinguish two main, divergent trends in the structural complication of analysers, two successive, mutually complementary stages in their development, which constitute a single, functional architecture.

The analyser formations located at various levels of the axial part of the CNS and closely knit with the elements of the coordination mechanism correspond to the lower stage of development which occurs relatively early in phylogenesis. They take shape as the result of direct overgrowth of the coordination mechanism by elements of the analysers and make possible further complication and expansion of the coordination resources of the organism. We shall designate them as the **analyser-coordination mechanism** (Fig. 5, *II*).

The subglottal cerebral ganglia of invertebrates (see Fig. 2*A*) can be regarded as a rudimentary homologue of the analyser-coordination mechanism of vertebrates, in which it is already well-formed. In the least developed

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* By 'centralized nervous system' we understand the ganglia of invertebrates and the central nervous system of vertebrates.

vertebrates (Cyclostoma), the main mass of central switching neurons may still be counted as the coordination mechanism, but in fish there is a burgeoning of the analyser-coordination mechanism in all analyser areas (Fig. 6).

A higher level of development of the analysers, which can be characterized as the greatest constructive achievement of living nature, is represented by **analyser systems** in the proper sense of the term. These systems (as already noted) consist of complex chains of switches (Fig. 7) that penetrate the whole CNS and link the perceptive surfaces of the sense organs with the highest cerebral ends of the analysers (which constitute the phylogenetically youngest supra-axial sections of the brain—see below) and are spatially differentiated from the analyser-coordination mechanism.

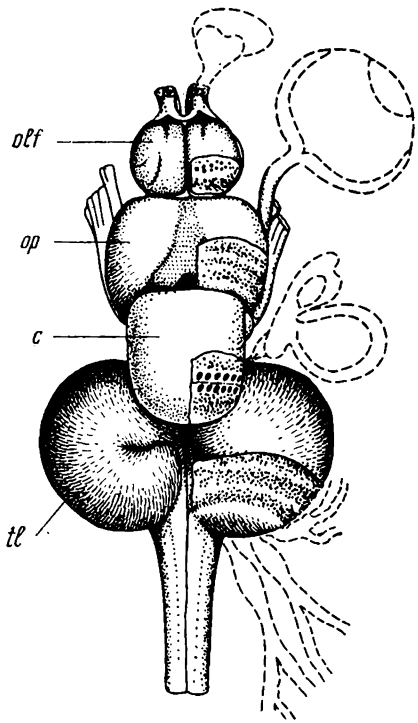


Fig. 6. Drawing of the brain of a fish (carp), showing the relation in the development of the cerebral parts of the various analysers. *olf*, olfactory lobe (fore-brain); *op*, optic lobe (mid-brain); *c*, cerebellum; *tl*, taste lobe of the medulla oblongata. On the right are represented a cross-sections through the indicated parts of the brain to illustrate the cortical type of the structure (in part after Herrick).

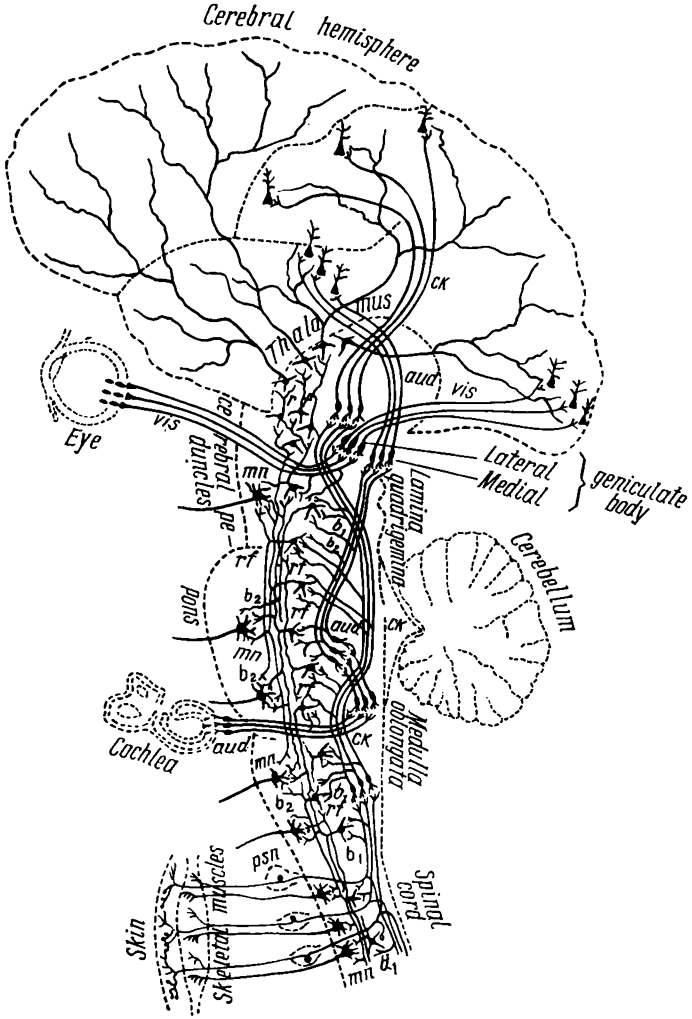


Fig. 7. Schematic drawing (with outline of the human brain) of the chief analyser systems and their connections with the coordination mechanism. Sensory organs, neuron switches in the upper and lower sub-cortex, and the cortical zones of the analyser systems are shown; *vis*, system of the visual analyser; *aud*, auditory system; *ck*, cutaneous and kinaesthetic systems (body sensation); *ps*, peripheral sensory neurons of the ganglia of the spinal and cranial nerves; *mn*, motor (effector) neurons of the spinal cord and brain-stem; *rf*, switching neurons of the reticular formation ($mn + rf$ = the coordination mechanism); b_1, branches along the analyser systems to the reticular and effector neurons; nb_2, end branchings of axons of the reticular neurons, contacting motor neurons (with partial utilization of our own scheme of 1959).

The phenomena of reflex activity, in which both the coordination and analyser-coordination mechanisms are involved, we group together as a single, common class of reflex coordinations. The two mechanisms (which constitute the axial part of the CNS) are jointly responsible for physiologically ordered responses to stimulation; but they are still insufficient to bring about integrated behaviour.

The reflex coordinations effected along the length of the axial part of the CNS embrace the sum total of the organism's separate reflex adaptations to its conditions of existence. They are the individual 'blocks' from which both the vital reactions inherited by the organism from its ancestors and those it has acquired during its own life are built up (reactions connected with its general orientation to its environment, the finding of food, self-defence, continuation of the species, etc.). The sum total of the interconnected reactions programmed in the supra-axial part of the CNS constitutes the integrated behaviour of the organism.

In the evolution of vertebrates it is possible to trace the growing complexity of reflex coordinations very clearly as they ascend the axis of the CNS, as the functional connections between the cerebral parts of the various analysers become more complex. In both phylogenesis and ontogenesis the 'stock' of the organism's effector activities (as Bernstein puts it) becomes richer and richer.

The analyser systems include those sections of the neuronal organization that are differentiated last in the course of evolution and that achieve the greatest structural and functional perfection and most intensive tempo of development. They only become clearly delineated in those vertebrates that have completed the transition from living in a homogeneous, watery medium to a more variegated terrestrial way of life (amphibia, reptiles). The greatest development and complexity in their structural and functional differentiation are achieved in the higher mammals, especially in man.

Unlike the coordination and analyser-coordination mechanisms the higher cerebral ends of the analyser systems pass beyond the confines of the axial part of the centralized nervous system and form its supra-axial part, which consists of an assemblage of 'pure' analyser neurons and their

interconnections, while the axial part consists of neurons of the analysers lying check-by-jowl with those of the coordination mechanism (Fig. 8).

In the higher invertebrates the still comparatively weakly developed supra-axial part is the supra-glottal cerebral ganglia mentioned above (see Fig. 2*A*). In vertebrates it is mainly formed by the end-brain from which the cerebral hemispheres are developed (see Figs. 2*B* and 4) with their rapid differentiation in the phylogenesis of higher vertebrates (mammals) into cortical and subcortical formations (see Fig. 5).

Reptiles, finally adapted to a land existence, are capable compared with amphibia of more differentiated perception of external influences and of using the parts of their bodies in a more differentiated way. Correspondingly they are the first vertebrates to display not only a greater refinement of the axial mechanisms for reflex coordinations, but also a clearly expressed differentiation of the supra-axial part of the CNS into cortical and subcortical structures.

In the higher vertebrates (mammals) the higher cortical ends of the analyser systems are represented by formations of the fully developed neocortex (see Fig. 24) derived last in phylogenesis and displaying the finest differentiation into layers (see Plate I*D*). These parts of the brain form the morphological background on which is projected the complex tracery of the mosaic of excitory and inhibitory points evoked by the action of various combinations of stimuli (objects) on the receptor surfaces of the sense organs.

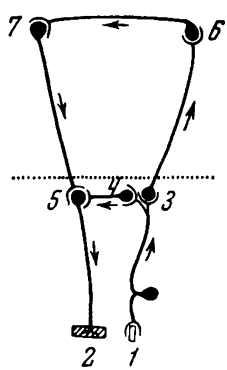
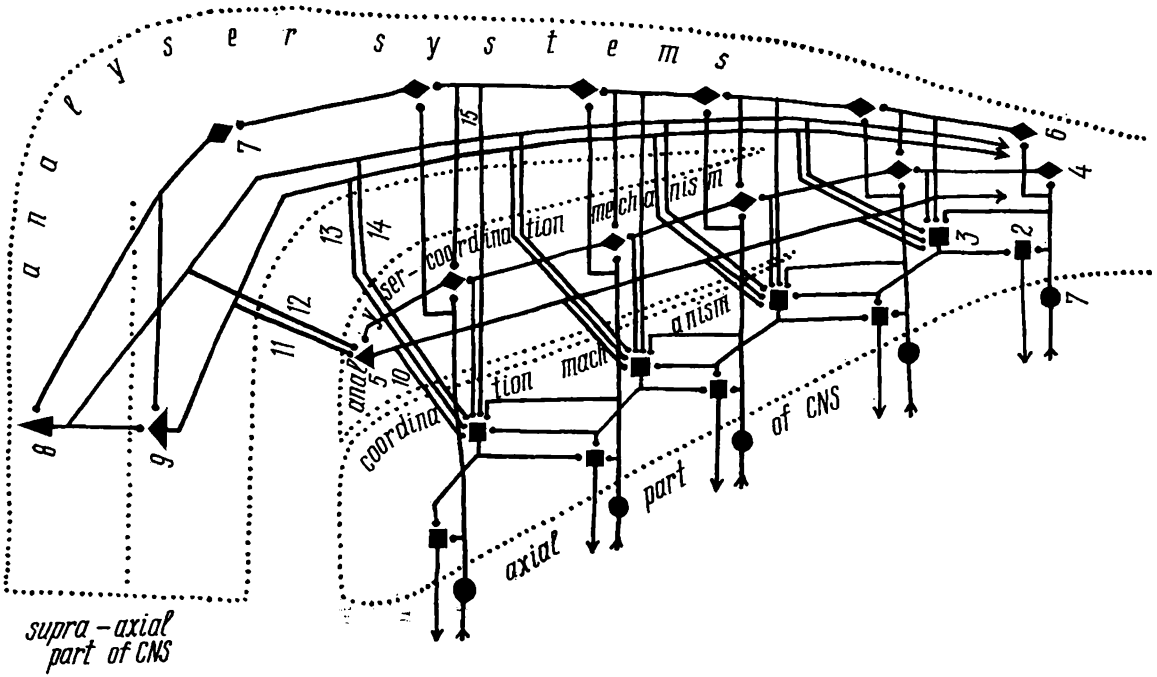


Fig. 8. Diagram of switches in the axial and supra-axial parts of the CNS (cf. Fig. 2*B*). The dotted line marks the boundary between the two parts: *1*, receptor; *2*, effector; *3*, neuron switching centripetal impulses to the supra-axial part of the CNS; *4*, neuron switching centripetal impulses in the axial part; *5*, motor (effector) neuron; *6*, neuron switching centripetal impulses in the supra-axial part; *7*, neuron in the supra-axial part conducting centrifugal impulses to a motor neuron in the axial part. It can be seen that the supra-axial part contains only the elements of analysers, while the axial part contains both these neurons (*3*) and neurons of the coordination mechanism (*4*, *5*).

Fig. 9. Diagram of the main divisions of the CNS (see also Fig. 21); *1*, peripheral sensory neurons relaying impulses from receptors; *2*, motor neurons innervating effectors; *3*, reticular neurons coordinating the interaction of motoneurons in the performance of local (segmental) reflexes of the spinal cord and brain-stem (axial part of the CNS, both motor and reticular neurons forming part of the coordination mechanism); *4*, neurons incorporated in the chains of switches located along the axial part of the CNS and relaying centripetal impulses in the sections of analysers forming part of the analyser-coordination mechanism; *5*, neurons forming part of the most highly organized sections of the analyser-coordination mechanism, which achieve a structure of cortical type (cortex of the superior colliculi of the mid-brain and of the cerebellum); *6*, neurons forming part of the chains of switches located along the axial part of the CNS and relaying centripetal impulses in the analyser systems; *7*, neurons forming part of the switching stations of the analyser systems located at the transition of the axial to the supra-axial part of the CNS and lying closest to the cerebral hemispheres (thalamus and geniculate bodies); *8*, neurons forming part of the phylogenetically newest and most complexly organized sections of the higher cerebral ends of the analyser systems (formations of the neocortex); *9*, neurons forming part of the evolutionary older (cortical and subcortical) sections of the higher cerebral ends of the analyser systems located in the supra-axial part of the CNS; *10*, pathways conducting centrifugal impulses from neurons of the analyser-coordination mechanism to those of the coordination mechanism; *11*, *12*, pathways conducting centrifugal impulses from neurons of the cerebral ends of the analyser systems located in the supra-axial part of the CNS to neurons of the analyser-coordination mechanism; *13*, *14*, the same, but conducting centrifugal impulses to neurons of the coordination mechanism; *15*, pathways conducting partly centripetal impulses spreading along the axial part of the CNS via the chains of switches of the analyser systems to neurons of the analyser-coordination and coordination mechanisms. Pathways conducting centripetal impulses spreading through the chains of switches of the analyser-coordination mechanism to neurons of the coordination mechanism are also represented on the diagram but not separately designated. To simplify matters the approaches to the coordination mechanism are represented only in respect of neurons of the reticular formations.


analyser systems
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axial part of CNS
coordination mechanism
analyser-coordination mechanism
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The highest level of development and perfection of organization is achieved in the cortical formations of the primates among mammals, and of man among the primates.

With these brain structures, the basic functional purpose of which is to determine the signal significance of multiform combinations of stimuli changing rapidly in time and space, is linked the reproduction of brain models, i.e. of images of things, phenomena, and situations, and concepts of them. On the basis of these models operations of varying degrees of complexity on the objects of the external world are programmed. By providing the organism with the fullest, all-round and ordered information about its surroundings the higher cerebral ends of the analyser systems become the material basis for reactions that relate it most exactly and complexly as a whole to the external world. They play a decisive role in integrating the organism's various reflex adaptations (both those inherited by it from its ancestors and those established in the course of its own life) into behavioural wholes.

The following major elements can be distinguished in their activity:

(a) determination, by analysis and synthesis of stimulation, of the signal significance of stimuli and of the systems of relations between them;

(b) the programming of responses to stimulation through integration of the whole aggregate of signals, and biologically purposeful utilization of the whole fund of reflex coordinations;

(c) higher synthesis of the animal activities of the organism (those directed toward the external world) and its vegetative activities (those connected with its internal medium) in the course of its adaptation to changing conditions of existence.

All these, taken together, constitute behaviour.

Now let us examine in more detail some of the most important structural and functional features of these three basic divisions of the nervous system and their interconnections (Fig. 9; see also Fig. 21).

3. The Coordination Mechanism

The principal physiological task of the coordination mechanism, as we have already said, can be reduced on the whole to the process of working out orderly responses to the

direct action of definite combinations of vitally important stimuli.

The coordination mechanism performs animal and vegetative reflexes on, one might say, a local scale, anatomically related to the segmental reflex arcs of the axial part of the centralized nervous system. These reflexes include

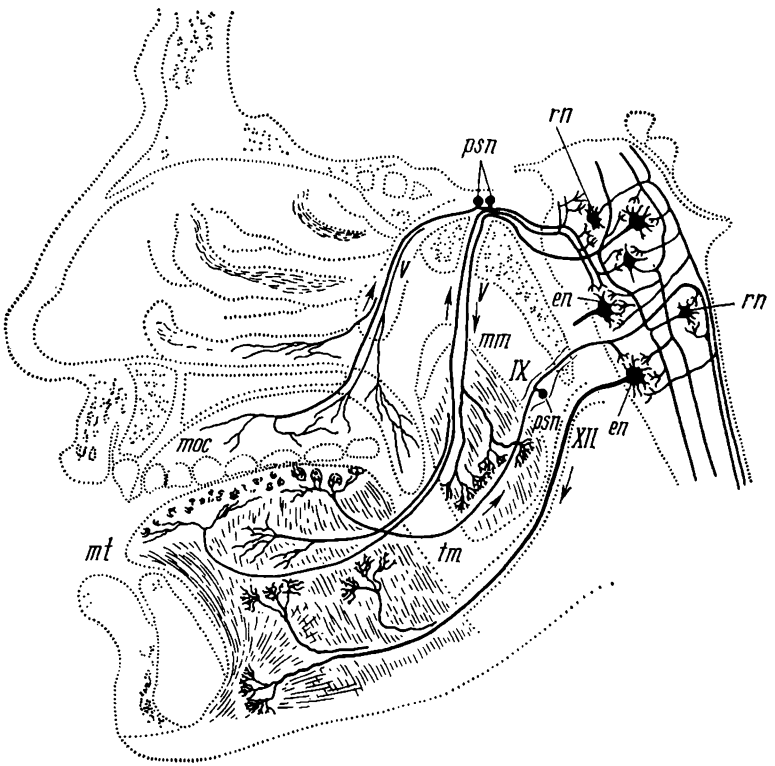


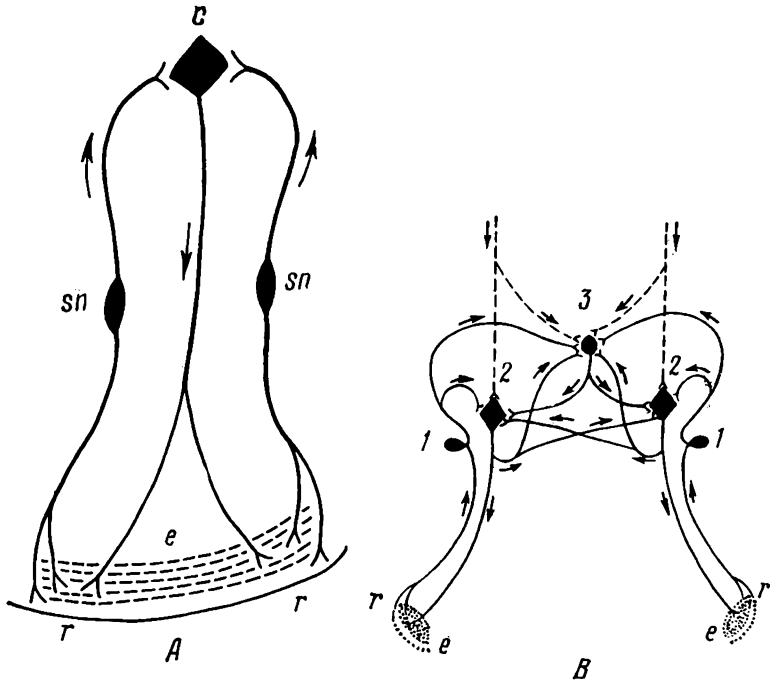
Fig. 10. Schematic representation of the connections among the elements by which reflex coordination of mastication is effected through stimulation of the mucosa of the mouth and tongue by food. Roman numerals designate the cranial nerves involved, carrying centripetal and centrifugal impulses (as indicated by the arrows) (in part after the schemes of various authors): *mt*, mucosa of tongue; *moc*, mucosa of oral cavity; *tm*, muscles of tongue; *mm*, masticatory muscles; *psn*, peripheral sensory neuron; *rn*, internuncial (reticular) neuron; *en*, effector neuron.

local defensive and adaptational reactions, reactions linked with ingestion and digestion, the simpler constituents of such static and locomotor reactions as the cervical, vestibular, and anti-gravity (e.g. tendon) reflexes, the reflexes maintaining the tonus of the skeletal muscles, and those of support and alternating movement of the extremities. The receptive fields of these reflexes are relatively limited in area and are predominantly localized in those parts of the body and organs that are directly involved in responding to stimulation (Fig. 10).

The coordination mechanism, as we see, is primarily adapted to correlating groups of receptors with definite groups of effectors. As the central nervous organization is evolved in complexity the activity of the coordination mechanism became correspondingly more complicated: and through the structural transformations thus arising there developed the possibility of providing functional connections between the various reflex arcs along the whole axial part of the CNS.

The foundation of ordered reflex activity of any complexity—from the rhythmic pulsing of the umbrella of a medusa and the crawling movements of worms to the finest differentiated movements of the human hand, eye, or speech apparatus—is an arrangement working on the principle of 'action and counter-action', that is, working on the lines of a conjugated functional pair of agonist and antagonist. This principle was established by Vvedensky and elaborated by Sherrington as the rule for reciprocal innervation (Fig. 11*B*). Physiologically it is adapted in the most developed way, as a result of strictly synchronized interaction of the processes of excitation and inhibition of both members of the conjugate pair, to perform coordinated movements based on the simultaneous switching on of the effectors of the agonist and on switching off of the effectors of the opposing antagonist. The role of the synergic muscles in this process consists in taking up the slack in the freedom of movement of an organ through their fixational tension, with the result that the possibility of movement in a definite direction is ensured.

There are grounds for supposing that the establishment of reflex activity both in the evolution of the animal kingdom and in the individual development of the organism during its intra- and extra-uterine life is directly linked



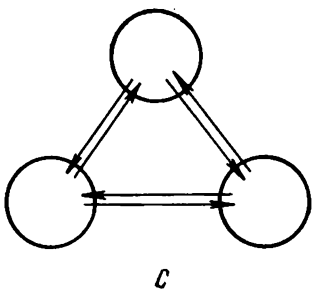


Fig. 11. *A*, scheme of the simplest coordination arrangement in a lower multicellular organism; *r*, receptor; *e*, effector (muscle system); *sn*, sensory neuron; *c*, neuron still combining the functions of effector and internuncial elements; *B*, scheme of an elementary coordination arrangement working on the principle of conjugate functional pair of agonist and antagonist; *r*, receptor; *e*, effector; (*1*) peripheral sensory neurons transmitting centripetal (afferent) impulses from receptors both to (*2*) effector (motor) neuron and to (*3*) an internuncial (reticular) neuron; the last, as indicated in the diagram, terminates in branchings of its nerve fibre (axon) at both effector neurons. The elements of feed-back are represented by the side and recurrent collaterals of the axons of the effector neurons. Arrows indicate the direction of movement of nerve impulses. Broken lines show descending (centrifugal) conductors passing through their terminal ramifications both to the effector and internuncial neurons; *C*, geometrical diagram of the two-way functional interrelations between the three central neurons of an elementary coordination device as an auto-regulating system.

with the formation of this physiological mechanism of conjugate functional pair.

Two stages, at least, of successive complication of the interactions between receptors, neurons, and effectors, can be distinguished in evolution, leading to structural differentiation of a mechanism.

Certain lower multicellular animals would seem to have a simpler apparatus that still works on the principle of simple alternation of the switching-on and switching-off of the one and the same group of effectors (see Fig. 11*A*). It is in that way, it must be presumed, that the rhythmic contraction and relaxation of the umbrella of a medusa, by which it achieves locomotion, is brought about. It has an interlacing of radial and circular bands of muscle fibres that contract and relax simultaneously as a result of impulses of excitation spreading throughout its whole nerve network, which immediately take over and switch on all the effector elements of the body. Their switching-off follows automatically after the switching-on. This primitive device already combines, consequently, the physiological properties of conjugate agonist-antagonist pair in the activity of a common group of effectors.

The structural differentiation of both the effector members of the pair, with corresponding transformations in receptor and neuronal organization, is plainly to be seen at the stage of evolution represented by worms (Fig. 12). These animals, which are adapted to the more complex conditions of terrestrial life, are able to perform more varied locomotor acts than medusae. In the epidermal-muscle sac of the worm two anatomically distinct groups of muscle fibres are distinguished, differing in the effect of the action performed by them. One group consists of circular fibres and the other of longitudinal fibres lying parallel to the axis of the body. Contraction of the circular fibres has the effect of elongating the body, while contraction of the longitudinal ones leads on the contrary to its shortening. The rhythmic succession of the coordinated crawling movements of a worm is already effected by a mechanism of alternate, synchronized, switching-on of the one group of muscles and switching-off of the other, i.e. on the principle of relations of reciprocal innervation between agonist and antagonist.

In complexly constructed animal organisms this prin-

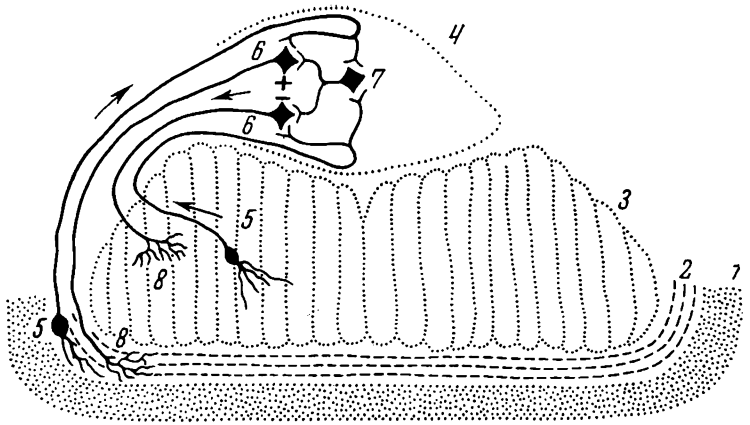
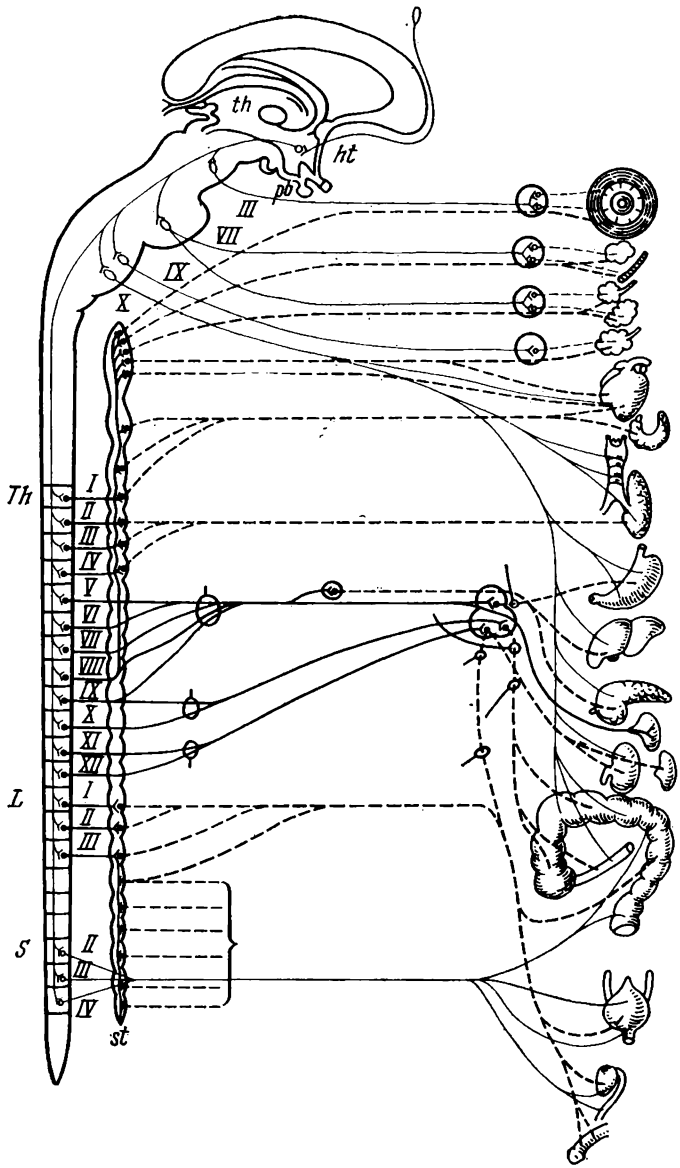


Fig. 12. Schematic picture of the arrangement of a conjugate, functional agonist-antagonist pair in a worm. *1*, skin cover of the body; *2*, layer of circular muscles elongating the body; *3*, layer of longitudinal muscles shortening the body; *4*, ganglion; *5*, peripheral sensory neuron; *6*, effector neuron; *7*, internuncial neuron; *8*, motor ending in muscle.

ciple is seen most clearly in the dual innervation (sympathetic and parasympathetic) of all their internal organs and systems of vital activity (Fig. 13). In the phylogenetically oldest physiological auto-regulations on which the life of the body directly depends, the functional relationship between the two members of the auto-regulating pair developed by evolution has been fixed.

Synchronized connections between agonist and antagonist also underlie all coordinated motor acts, both voluntary and involuntary, in the reactions of the organism to external stimulation; and the mechanism of reciprocal innervation in functional relations is much more mobile in the sphere of its interconnections with its external surroundings than in the sphere of internal auto-regulation, bringing many different skeletal muscles into simultaneous and consecutive joint activity in a variety of combinations.

For an understanding of the formation of coordinated reflex acts in the individual life of the organism, the functional reorganizations that are observed with cross-suturing of the tendons of agonist and antagonist muscles, or of the nerves innervating them (Bethe, 1926; Asratian, 1953; and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others), are of great interest. It has been shown, for example, that when the flexor muscles of an extremity are linked to the nerve centres of the extensor muscles and *vice versa*, then at first they work in an uncoordinated way. But later a physiological mechanism of the type of agonist and antagonist that synchronizes the activity of flexors and extensors is gradually re-established.

It is particularly interesting that biologically appropriate utilization of the organism's effector apparatuses is thus fully restored in the performance of one adaptive reaction or another. In the appropriate conditions the organism responds as before the operation with reactions adequate to the stimulation, despite the radical alteration in the relations between its nerve centres and the organs innervated by them. Also of interest is the circumstance that the new coordination relations appeared to be effective in the stimuli coming from the higher sections of the CNS (with stimulation of the cerebral cortex).

To revert to the special features of the construction of the coordination mechanism, let us note the following.

The conjugate agonist-antagonist pair can be regarded as an elementary coordination device, a kind of primitive fragment of the coordination mechanism as a whole. As can be seen from the diagram in Fig. 11*B*, the input side of the device is formed by the pair of receptor elements and the peripheral sensory neurons linked with them, which are exclusively specialized for the function of conducting impulses from receptors to the central neurons. The output side is represented by the corresponding pair of effectors (striped skeletal muscles, smooth muscles of the internal organs). The central part, which performs the most responsible function of the device, consists of a combination of

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Fig. 13. Dual vegetative innervation of internal organs. Fibres of the sympathetic system running to organs are indicated by broken lines; the parasympathetic system is depicted by continuous lines. The distribution of ganglia along the sympathetic trunk (*st*) and of sympathetic ganglia and plexuses in the area of the head and in the internal cavities of the body is shown; *th*, thalamus; *ht*, hypothalamus; *pb*, pituitary body (hypophysis). Roman numerals designate the cranial nerves and the roots of the various segments of the spinal cord.

three elements, the central neurons. In essence, then, in addition to the two motor (effector) neurons directly innervating the corresponding effectors, there is a special neuron as a third element (intermediate or intercalary), known as an internuncial neuron.

The three central neurons making up the combination just described and forming, as we shall see below (see Chapter II, section 3), the central link in the auto-regulatory system, are so connected that each of them can influence the other two, and itself be influenced by them (see Fig. 11*C*). The interaction of the impulses circulating in this elementary section of the neuronal network conditions the physiological mechanism of summation and interference of excitations in the nerve centres. According to the latest electrophysiological research (see Chapter III, section 3) the neurons assigned by us to the group of internuncial neurons take an active part in the process. In particular it has been shown that elements of this kind, unlike the effector (motor) neurons, are characterized by a very low threshold of excitability and can respond to a single afferent stimulus by generating rhythmic, high-frequency discharges up to 1000 or more impulses per second. This transformation of a single stimulus into high-frequency discharges would seem to be of essential significance in determining the functional state of the effector neurons forming part of the central switching apparatus. On the impulses generated by the internuncial neurons directly depend the changes in excitability of the effector neurons that determine the critical point or threshold of their transition from a state of excitation to one of inhibition, and *vice versa*.

There are grounds for supposing that no one ordered reflex act can be brought about solely by the effector neurons, without the participation of the internuncial neurons 'added' to them. Elements of this kind, with the recurrent collaterals of the axons of effector neurons (see Fig. 11*B*), play an essential role in distributing afferent impulses to the appropriate groups of effector neurons, and also in closing the circuits in which impulses circulate (see Chapter IV, section 2) during their transmission from receptors to effectors.

Through a corresponding organization of connections between the peripheral neurons conducting impulses from receptors, the effector neurons, and the internuncial neuron,

the last-named concentrates in itself the through and return connections of both the reflex arcs conjugated in a paired functional system. When the physiological parameters of all the components of this arrangement are selected and mutually coordinated in a certain way, the internuncial neuron takes on the quality of a functionally very mobile unit, influencing the distribution of states of excitation and inhibition between the agonist and antagonist centres and regulating the reciprocal switching-on of some effectors and switching-off of others.

The internuncial neuron plays the role, in the functioning of any coordination device, of an element making a confrontation, collation, and comparison of simultaneously and consecutively acting stimuli, and of the reactions caused by them in the effector ends of both reflex arcs. As can be seen from our diagram (Fig. 11*B*) the functioning of this element involves a correlation, on the principle of feed-back, of signals to act with information on the action actually being performed.

Signals coming from the higher parts of the central nervous system, like those arriving from the periphery, are simultaneously addressed both to the executive elements of the reflex arcs (effector neurons), and to the internuncial neuron (see Fig. 11*B*). As a result of this organization of connections between neurons, the auto-regulatory physiological system involved in the corresponding section of the coordination mechanism comes under the influence of the higher instances of the brain.

There are a number of morphological facts to back up this conception. In particular it has been established that the terminal branchings of both the centripetal fibres coming from the periphery and the centrifugal ones descending from the higher parts of the CNS pass not only to the effector, but also to the internuncial, neurons of the spinal cord and brain-stem (Fig. 43*C*). This has been demonstrated in one of the most important pathways of the central nervous system, the cortico-motor (or so-called pyramidal) tract by way of which the impulses of voluntary movements are transmitted.

The combination of three central neurons (two effectors and one internuncial) that constitutes the elementary unit of the coordination mechanism can be regarded as a structure that would seem to correspond in the highest degree in its

properties and effective potentialities to the working principle of the optimum regulator.

It can be supposed that, like the last-named, this system of two-way interconnected neurons is able independently to find and perform the optimum variants for every reaction of the functional states of its separate elements and their interactions.

The scheme outlined above may also underlie the function (universal to a nervous organization of any complexity) of closure of conditioned reflexes in which reflex arcs of conditioned or unconditioned stimuli operate as both members of a functional conjugate pair. A circumstance of great interest here is that we find an analogue of the internuncial neuron (Fig. 14) in schemes for experimental models of the establishment of conditioned reflexes together with elements for the direct transmission of impulses located along both 'reflex arcs' (the 'reinforced' and the 'reinforcing'). As has been shown by a number of recent electrophysiological researches (Gastaut, 1958; Fessard, 1962; and others) convergence of various afferent impulses onto internuncial (reticular—see below) neurons seems to play a definite role in realizing those elements of the closure function that take place at the subcortical levels of the CNS. Finally, this scheme can also be pictured as the prototype

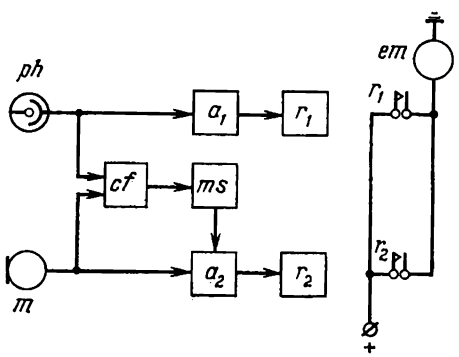


Fig. 14. 'Skeleton' scheme of the modelling of a conditioned reflex. *ph*, photo-elements; *m*, microphone; *a*, amplifier; *r*, relay; *em*, electric motor; *cf*, co-incidence filter; *ms*, memory store. In this layout the *cf* and *ms* elements play the role of an internuncial neuron, inserted between the two chains of direct transmission of impulses (ph—a_1—r_1, and m—a_2—r_2) (after Kraizmer, with modifications).

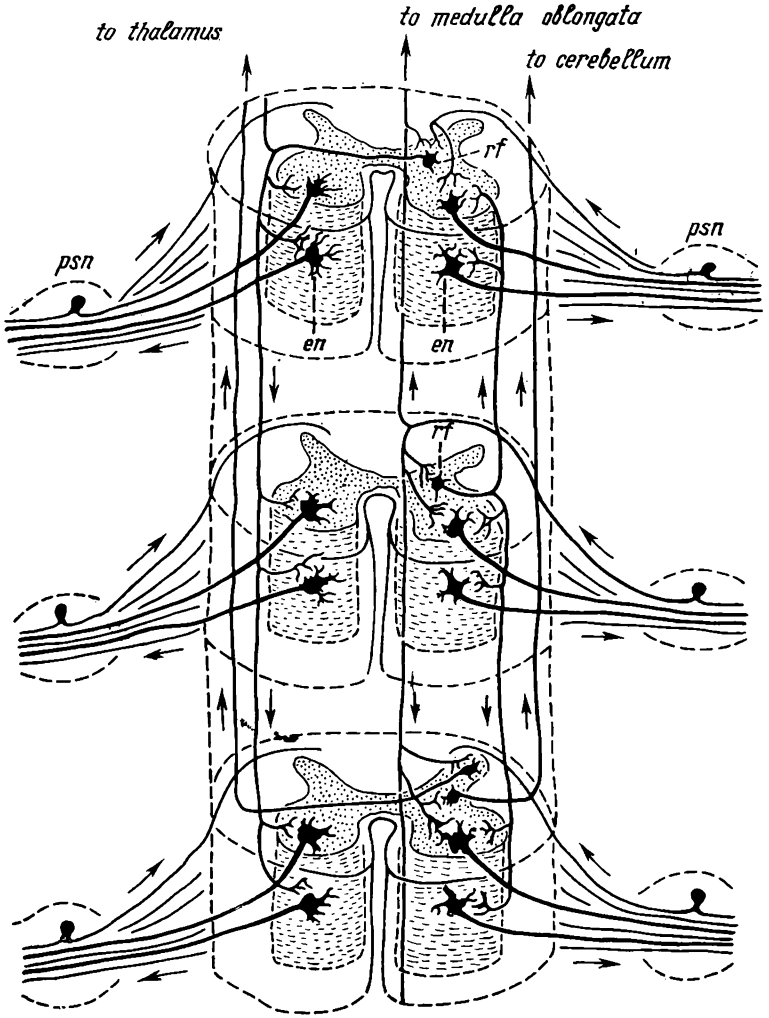


Fig. 15. Scheme of the intersegmental connections of the coordination mechanism. Three contiguous segments of the spinal cord are represented: *psn*, peripheral sensory neurons of the spinal ganglia; *rf*, neurons of the reticular formation distributing afferent impulses through various groups of effector (motor) neurons (*en*). Arrows indicate the direction of impulse flow. In addition to elements of the coordination mechanism, certain conducting pathways are also shown related to the analyser-coordination mechanism and the analyser systems (see the arrows indicating flow to the cerebellum, medulla oblongata, and thalamus).

of a 'logic' mechanism selecting a definite variant of action from two or more possibilities.

In actual nervous systems the assembly of internuncial neurons forms the reticular formation of the spinal cord and brain-stem (see Figs. 3, 4, and 7). At all stages of vertebrate evolution the aggregate of these neurons is a complex of intricately interconnected internuncial neurons constituting the most important integral part of local coordination reflex devices.

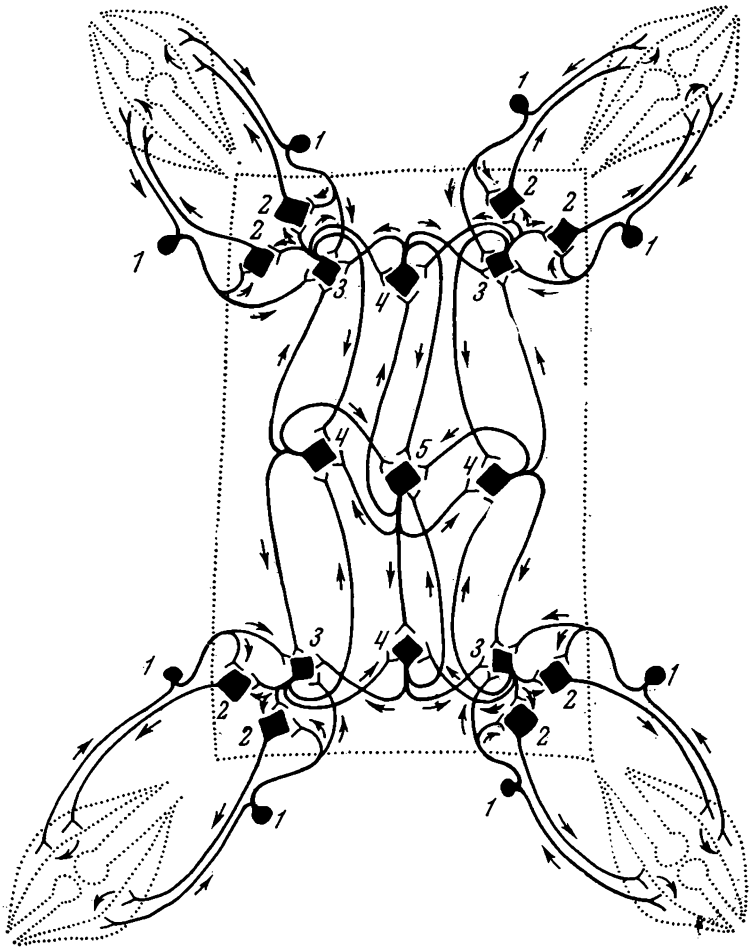
The neurons of the reticular formation take on the role of a 'clearing house', distributing impulses coming from receptors and other parts of the CNS through various groups of effector neurons located both at the same level and at various others of the axial part of the CNS (Fig. 15). Let us recall that it is precisely this formation that constitutes the axis of the CNS which is overgrown, in the course of evolution, by analysers.

It is of interest to ask how far complication of the function of the coordination mechanism can be carried by enriching it with reticular neurons and multiplying the connections between them and the effector neurons. In other words, to what degree can the 'organizational' possibilities inherent in the properties of the coordination mechanism itself be realized without additionally involving analysers in its reflex activities?

In the scheme suggested here (Fig. 16) complication of the interconnections of the reticular neurons is represented as complication of the locomotion that an animal can perform especially when all four extremities are involved in the coordinated and cooperative movements of walking, running, etc. Taking this scheme as our premise it can be suggested that the switching device of the reticular formation is in a state to embrace and unite in a single reflex act a greater or less number of separate segmental reflexes along the axis of the CNS. Physiological confirmation of this view is provided by the fact that a decapitated animal is still in a condition to perform coordinated locomotor movements.

The groups of reticular neurons, linked in a definite way along the whole length of the axial part of the CNS, form the suprasegmental apparatus of the coordination mechanism.

Study of the changes taking place in the CNS of vertebra-



F i g. 1 6. Scheme of the switching device of a part of the coordination mechanism serving harmonious movement of all four extremities. *1*, peripheral sensory neuron; *2*, effector neuron; *3*, *4*, *5*, internuncial (reticular) neurons. The central apparatus innervating each agonist-antagonist pair of an extremity includes a definite group of internuncial neurons of the first order (*3*; cf. *3* in Fig. 11*B*). Interaction of the two agonist-antagonist pairs of related pairs of extremities (the two front or hind legs, or the two left or right legs) is realized by way of an additional group of internuncial neurons of the second order (*4*). Interaction of the agonist-antagonist pairs of all the extremities takes place through yet another supplementary group of internuncial neurons, this time of the third order (*5*) and located in a central position. All these groups of internuncial neurons are functionally connected by closed circuits of circulating impulses.

tes during the course of evolution also permits us to conclude that complication of the system of reticular neurons has its own limits. With the further complication of animal reflex coordinations, in connection with the development of analysers, certain suprasegmental sections of the coordination mechanism connected with complex reflex acts are gradually transformed into constituent parts of the analyser-coordination mechanism.

Recent research in experimental morphology by Zhukova and Leontovich (1964) has shown that the reticular formation also extends to the phylogenetically older sectors of the supra-axial part of the CNS lying at the base of the brain. These sectors, which are a direct continuation of the axial part of the CNS, include in particular the hypothalamic region of the between-brain (see Fig. 4) and certain ancient formations of what Filimonov calls the cortex semiseparatus, and the subcortical formations contiguous to it (see Fig. 5, *ofc*, *sg*). All the structures mentioned predominate in lower vertebrates with still weakly developed endbrains and quite undeveloped cerebral hemispheres (e.g. cyclostomes and fish).

Apart from the various segmental animal reflexes round of 'service duties' of the coordination mechanism also includes the performance, as mentioned above, of vegetative reactions. The reflex coordinations located along the axial part of the CNS (which are related to the systems of internal life activity, and at the same time to the reactions to direct damage to body tissues that are connected with pain recepts) are concentrated in the coordination mechanism itself (Fig. 17). But these reflex coordinations are only slightly represented, it would seem, in the analyser-coordination mechanism. The fact that local vegetative reflexes, like local defence ones, are preserved in the integrity of the segmental arcs of the spinal cord and brainstem and of the reticular formation (the central apparatus of switches and connections uniting them) can be taken as substantiation of that conclusion.

Reflexes of a similar kind that can be included in this group are, in particular, the defence reflexes observed in certain lower vertebrates (e.g. fish and amphibians) in which the pigment colours of the skin change with alterations in the colour of the background on which the animal finds itself; the higher central representation of this reac-

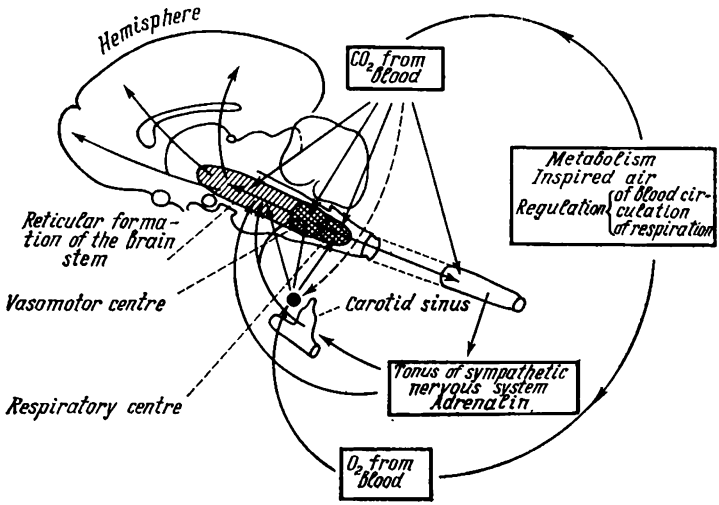
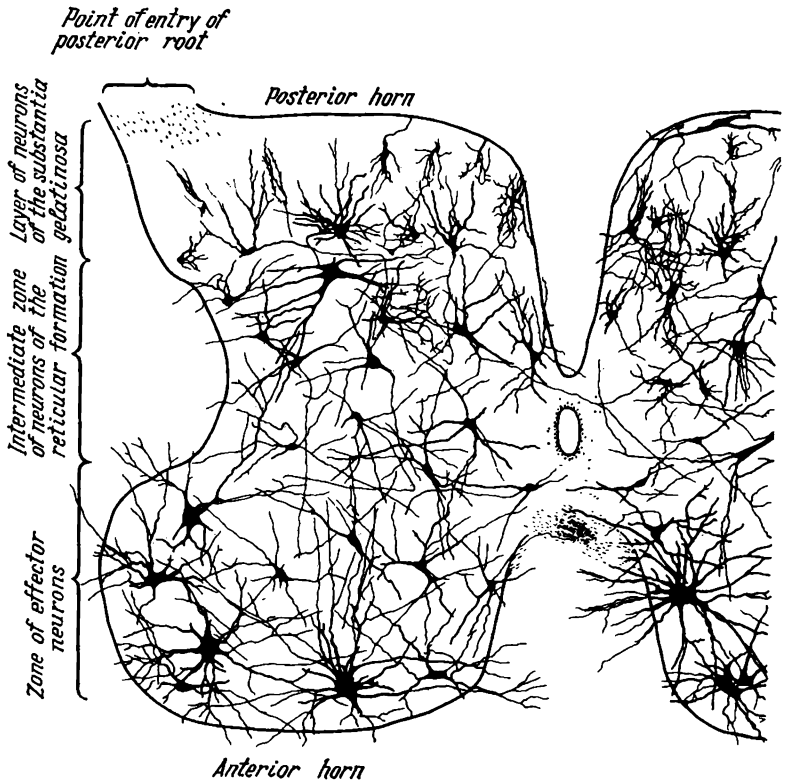


Fig. 17. Diagram illustrating the localization of the central representation of the organism's vegetative (respiratory, cardiovascular) functions in the reticular formation of the brain-stem (coordination mechanism). Certain auto-regulating physiological systems of the organism's internal medium, which are drawn into a functional circuit across the reticular formation of the brain-stem and spinal cord, are shown. The influence of the reticular formation of the brain-stem on higher supra-axial parts of the CNS (the cerebral hemispheres) and lower ones (the spinal cord) is also shown; ascending influences from the reticular formation of the brain-stem are incorporated in the concept of a diffuse activating, or non-specific, system (after Delloux and Bonvaillier).

tion is apparently located in the hypothalamic region of the between-brain. The reflex arc itself can be represented as follows: the retina of the eye, as the point of application of stimulation; the optic nerve, and the nuclei of the hypothalamic area; from there impulses are passed further, partly to vegetative centres in the brain-stem and partly via the hypophysis to the system of endocrine glands that are involved, along with the vegetative nervous system, in the pigment reactions of the skin. The retino-motor effect in the retina of frogs during illumination of the skin must also be taken as a peculiar specialized manifestation of the functioning of the coordination mechanism. Certain researchers (Biryukov, 1960) note the significance of light stimulation in maintaining the general tonus of the skeletal

muscles (phototonic function of the receptor part of the visual analyser).

The central grey matter lining the cavity of the fourth ventricle and the sylvian aqueduct and continuing directly into the nuclei of the hypothalamic region must also be considered anatomically a part of the coordination mechanism. That formation also consists of neurons of the reticular type (Zhukova, 1964), and can be considered, from the physiological aspect, mainly as the central representation of the various vegetative auto-regulations of the orga-


Point of entry of posterior root
Posterior horn
Layer of neurons of the substantia gelatinosa
Intermediate zone of neurons of the reticular formation
Zone of effector neurons
Anterior horn

F i g. 1 8. Map of the neuronal structure of the grey matter of the spinal cord (after Zhukova). The differences in fine structure of the neurons that we assign to the analyser-coordination mechanism (substantia gelatinosa) and of the neurons of the reticular formation and motor neurons that make up the coordination mechanism are distinctly seen (see also Fig. 30).

nism. The central grey matter of the ventricles of the brain, which is particularly massive in amphibians, has—it must be thought—an essential role in the special vegetative adaptations of the organs and parts of the body to the conditions of their activity. The nuclei of the hypothalamic region (see Figs. 4 and 13) influence various aspects of the life activity of the whole organism, viz. its trophic and metabolic processes and the plastic processes of the renewal of living matter in cells and tissues.

The idea that a very important part of the organism's vegetative life (as the sum of the reflexes occurring in its internal medium) lies in the field of the coordination mechanism has also received confirmation from recent morphological research. It has been shown that the vegetative (sympathetic and parasympathetic) centres of the spinal cord and brain-stem (see Fig. 17), like the central grey matter of the ventricles and hypothalamic region, are formed of typical reticular neurons distinguished by their structural features from both motor neurons and the neurons forming the analysers (Zhukova and Leontovich, 1964) (see Figs. 18 and 30).

Thus it can be supposed that the central nervous apparatus processing signals from the internal medium of the organism has not been differentiated to any significant extent from the bulk of the coordination mechanism during the evolution of vertebrates. This category of reflex process performed in the body itself can only be indirectly linked with the activity of the analysers, a conclusion that accords well with the position held by many physiologists that interorecepts are much less represented in the cortex than recepts directly linked to the analyser systems.

4. The Analyser-coordination Mechanism

As its name implies the analyser-coordination mechanism is a complex formation consisting of an evolutionarily older part (the coordination mechanism) and a younger part (analysers).

As already recalled, the mechanism must include all the nodes of switches, and their connections, belonging to the lower cerebral parts of the analysers and directly overlaying the corresponding sections of the coordination mechanism, i.e. definite groups of neurons of the reticular

formation uniting local (segmental) reflex arcs along the axis of the CNS.

This mechanism is called upon to provide more complex reflex coordinations linked with some degree or other of orientation in the space about the organism. In particular it is concerned with orientational and adaptational reflexes, above all to visual and auditory stimulation (the reflexes self-tuning the analysers can also be included in this group), and then with static and locomotor reflexes and the reflexes that maintain the equilibrium of the body.

Neurons specially concerned with the processes of distributing tonus in the skeletal muscles in various positions and movements of the body play an important role in active orientation of the organism in the external world. Through joint activity of appropriate groups of neurons located at various levels of the axial part of the CNS rapid changes in the form of tonus and tension in the muscles of the body are brought about. This kind of reflex coordination, which also involves participation of the analyser-coordination mechanism, attains particularly great complexity in animals whose extremities possess many degrees of freedom of movement.

In contrast to the coordination mechanism, the analyser-coordination formations of the brain have much wider receptor fields located not only in adjacent parts of the body and organs but also in spatially remote ones.

A considerable part of the recepts most vitally concerned in effecting the complex reflexes about which we are speaking comes from the sense organs located around the head (the retina of the eye, the cochlea of the inner ear) and from the organ of equilibrium and spatial orientation (the vestibulary and otolithic apparatus of the inner ear). This circumstance also explains why the main burden of central processing of the corresponding signals falls on the brain-stem, where the analyser-coordination formations reach their fullest development. The optic lobes of lower vertebrates (see Fig. 6) and of birds, which correspond to the anterior (or superior) colliculi of the mid-brain of mammals, belong to it; the cerebellum is also one of these formations, together with its extensive system of two-way connections (see Figs. 23 and 26), and the vestibular and other nuclei located in the brain-stem that distribute tonus in the skeletal musculature in various positions and move-

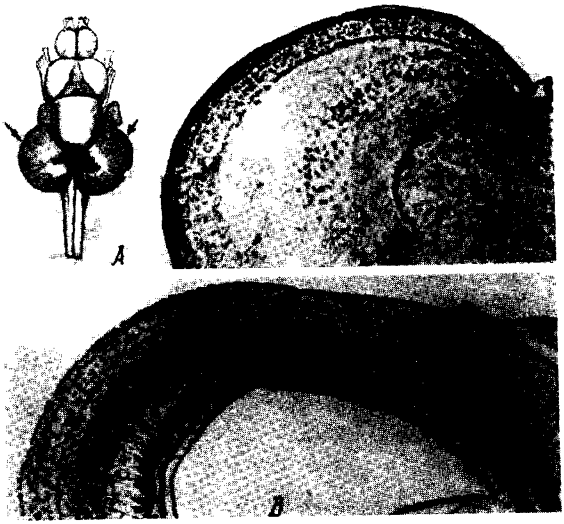
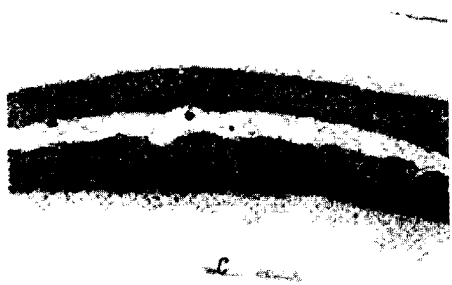
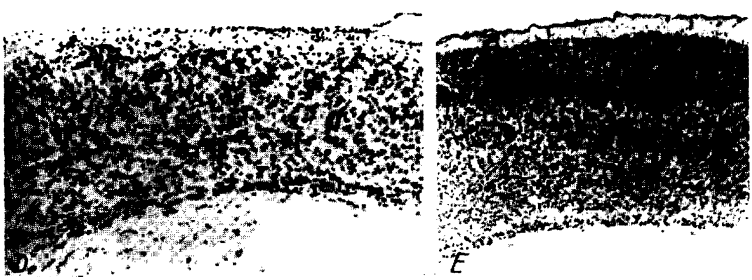


Plate I. Various forms of structure of cortical (layered-screen) type in analysers *A*, taste lobe of a fish (at the left of the photomicrograph is a drawing of a fish brain with arrows indicating the taste lobes); *B*, optic lobe of the mid-brain in a lizard; *C*, cerebellar cortex of a bird; *D*, auditory nucleus of the medulla oblongata of a mouse (with a structure of cortical type); *E*, fully developed neocortex of the cerebral hemispheres of a white rat (*A*, *B*, *C*, and *D* after Svetukhina; *E*, after Zvorykin).





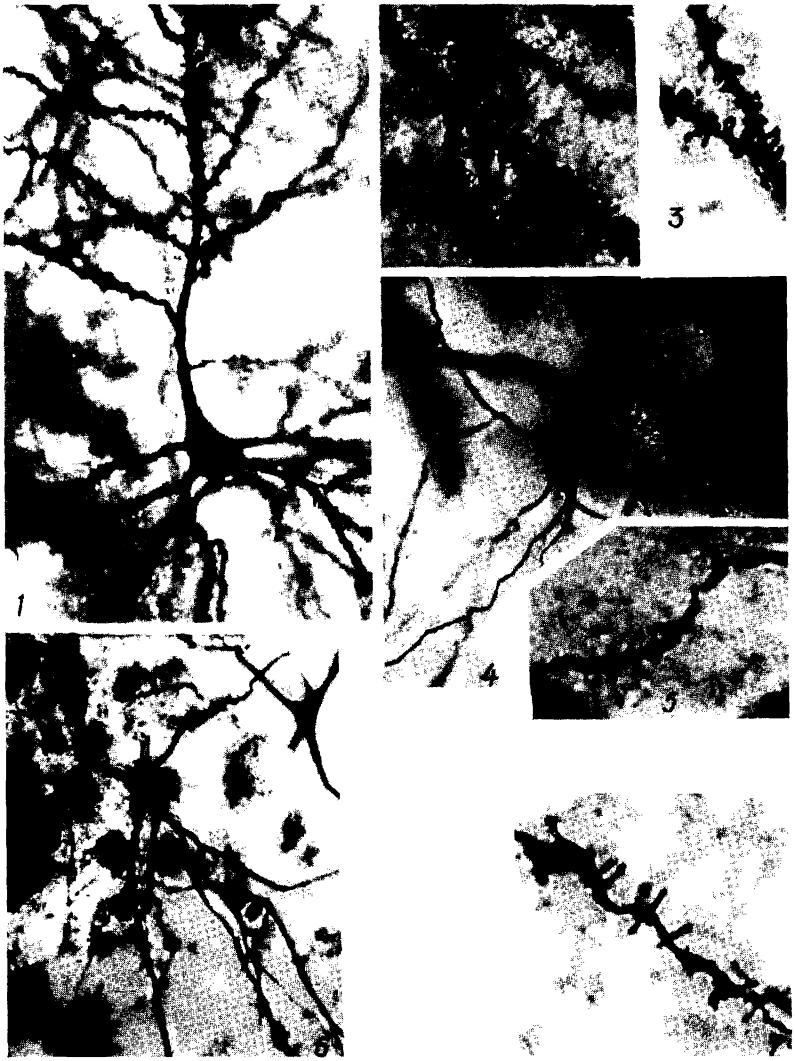


Plate II. Fine details of the structure of dendrites of pyramidal and stellate cells of the cerebral cortex, and of reticular neurons. Photomicrographs from preparations: *1*, pyramidal cell; *2*, dendrites of pyramidal cells covered with numerous short side appendages; *3*, dendrites of similar structure of an efferent cell with long axon from a subcortical ganglion; *4*, short-axon stellate cell of the cortex with smooth, spineless dendrites; *5*, dendrite of a stellate cell, with rare, much elongated appendages; *6*, reticular neuron of the medulla oblongata; *7*, dendrite of a reticular neuron, with rare and much elongated appendages (spines) (*1*, *2*, *4*, *5*, after Poliakov, 1953-61; *6*, after Zhukova, 1959; *3*, *7*, after Leontovich, 1959).

ments of the body. In certain bottom-feeding fish with a highly developed sense of taste, the taste lobes of the medulla oblongata attain immense size (see Fig. 6), and are one of the most important divisions of the analyser-coordination mechanism.

It may be noted in passing that the service of maintaining body equilibrium, which is significantly represented in the axial part of the CNS by several vestibular nuclei and their connections with the cerebellum and motor centres of the eye muscles and skeletal musculature of the whole body, does not extend beyond the level of the analyser-coordination mechanism (which would explain the absence of a clearly delineated representation of the vestibular system in the cerebral cortex).

There are grounds for considering that the analyser-coordination mechanism is represented not only in the brainstem but also in the spinal cord where the layer of switching neurons concentrated in the substantia gelatinosa (Fig. 18) (which is located at the point of entry of the sensory fibres of the posterior roots) can be regarded as its analogue. The substantia gelatinosa of the spinal cord is continuous with that of the medulla oblongata which is concentrated along the roots of the sensory nuclei of certain cranial nerves.

The layer of neurons in the substantia gelatinosa is superimposed upon the coordination mechanism like an additional zone of switches on the pathway of centripetal (afferent) impulses coming from the periphery and then being distributed via the reticular neurons of the grey matter of the spinal cord among the various groups of executive (effector) neurons (see Fig. 15). The elements involved, of course, are adjusted for the more finely differentiated reflex closures completed directly at the segmental level of the spinal cord itself.

The switches in the substantia gelatinosa are essential for coordinating the flow of a variety of local (mainly locomotor) reflexes effected by means of the highly mobile polyarticulated extremities. In mammals the neurons of the substantia gelatinosa, like those of the analyser-coordination formations lying higher on the axis of the CNS, are directly involved in performing the differentiated movements of the trunk and extremities effected by stimulation arriving from the cortex.

As Zhukova's research (1960) has shown, the substantia gelatinosa (which performs the function of an integrating apparatus working at the level of the spinal cord) has peculiar features of neuronal structure that to a certain extent make it resemble the cortical formations built on a layered-screen pattern (see below). In this zone of the grey matter of the posterior horn of the spinal cord (see Fig. 18) a spatially orientated, geometrically ordered distribution of neurons has definitely been observed. Another characteristic is the presence of neurons with short axons, or forms resembling them in the structure of their axon and dendrite ramifications.

The terminal branchings of the axons of these neurons form contacts with neighbouring cells, which is typical of the switching stations of the analysers. As Zhukova has also noted, it can be supposed from the data in the literature that there is a localization of a somato-topical type of organization in the substantia gelatinosa of projections of the receptor periphery that perceives cutaneous and kinaesthetic stimulation in areas of the corresponding segments of the spinal cord. These facts confirm our idea of the substantia gelatinosa as a division of the analyser-coordination mechanism.

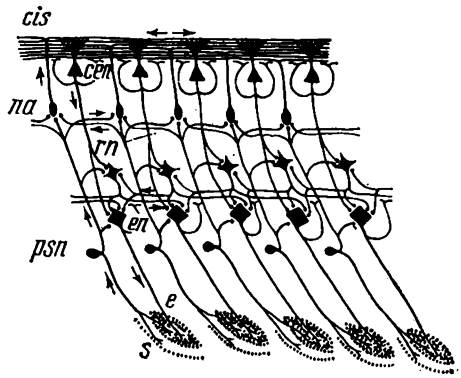
The next structural feature is characteristic of the brain parts of the analysers in both the axial and the supra-axial sections of the CNS. What we have in mind are the structures belonging to the most complexly organized divisions both of the analyser-coordination mechanism and of the analyser systems. The cerebral part of any analyser, at whatever level of the CNS it is located, always acquires a structure of a layered-screen or cortical type (Fig. 19) as it attains a definite degree of complexity in the processes of analysis and synthesis of stimulation performed in it.

We find these structures being formed, for example, in the taste centres of the medulla oblongata of fish with a highly developed sense of taste (see Fig. 6 and Plate I*A*). In animals capable of perceiving ultrasonic vibrations (certain rodents, carnivores, and pinnipeds) the primary auditory centres of the medulla oblongata have a similar neuronal structure (Plate I*D*). In all vertebrates a structure of cortical type develops characteristically in the optic lobes (the anterior colliculi) of the mid-brain (see Fig. 6 and

Plate I*B*) and in the cerebellum (Plate I*C*) The cortex of both these formations can be regarded as the prototype as regards the features of its neuronal organization of the cortex of the cerebral hemispheres (Plate I*E*).

The evolution of the cortical structure of the cerebellum has been brought about by the fact that this automatically functioning organ of the brain performs the analysis and synthesis of stimulation affecting the various receptor surfaces of the organism and provides very complex reflex coordinations involving the effector apparatuses of the whole body.

The higher cerebral ends of the analyser systems (which are formations of the neocortex of the cerebral hemispheres of phylogenetically later differentiation—see Figs. 22 and 24) attain their fullest development and complexity of structural differentiation of a cortical type in a number



F i g. 1 9. Diagram of the neuronal organization of the cerebral parts of the analysers and the underlying structure of cortical type. The drawing represents the complex of cutaneous and kinaesthetic analysers: *s*, receptor surface of skin; *e*, effector (striped muscle); *psn*, peripheral sensory neuron; *en*, effector neuron; *rn*, neuron of the reticular formation; *en*+*rn*, coordination mechanism; *na*, neuron forming part of the switching apparatus of the cerebral part of the analyser and adapted to transmit centripetal (afferent) impulses to the cortical apparatus; *cen*, cortical efferent neuron via which centrifugal impulses directed to the coordination mechanism are switched; *cis*, integrating system of horizontal (tangential) connections functionally uniting the efferent neurons of the cortex, and universal for all forms of organization of cortical type. This structural feature is a most essential aspect of formations of cortical type.

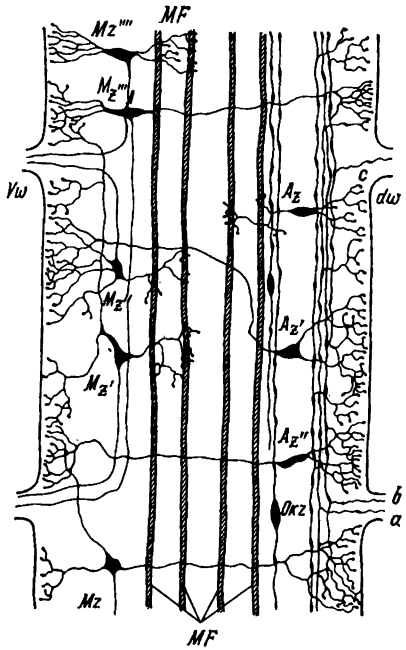


Fig. 20. A semi-schematic drawing of the neuronal structure of the spinal brain of a lower vertebrate (sand-eel); *a*, *b*, *c*, peripheral sensory fibres entering through posterior roots; *Mz*, effector (motor) neurons; *Az*, internuncial neurons (which we attribute to the reticular formation); *Mf*, longitudinally oriented thick nerve fibres. On the right is represented bundle of longitudinally oriented fine nerve fibres forming the continuation of fibres of the posterior roots. It will be seen that the dendrite ramifications of the neurons are perpendicular to the longitudinal fibres (after Tretyakov's data cited by Zavarzin).

of mammals. In lower vertebrates that still have a weakly developed end-brain without cerebral hemispheres, the axial analyser-coordination formations already show considerable complexity of structure of a cortical type (see Fig. 6 and Plate I), while still being represented in a rudimentary degree in the supra-axial part of the CNS by formations of the ancient cortex or cortex semiseparatus (Filimonov).

The transformation of the coordination mechanism into the analyser-coordination mechanism with its structures of cortical type can be clearly traced in the CNS of lower vertebrates in respect of the following features of neuronal organization.

A general feature of the organization of the spinal cord and brain of a lower vertebrate is the special form of spatial distribution of neurons and interneuronal connections, i.e. the zones of contact or synaptic articulations between neurons. A characteristic feature of this organization is that the elements so articulated lie in mutually perpendicular planes (Fig. 20). The dendrite ramifications of the effector and reticular neurons located in the axis of the CNS are

predominantly distributed transversely, at right angle to the bundles of nerve fibres contacting them, which are mainly oriented longitudinally, i.e. along the axis.

As a result of these topographical relations, within the whole system of interneuronal connections most favourable conditions are created for simultaneous and successive inclusion of the large groups of neurons forming the coordination mechanism in the waves of excitation spreading along the central conducting nerve pathways. In the same way fuller realization of the functional possibilities inherent in the coordination mechanism is achieved, which, as already indicated, is the supreme physiological task of the analyser-coordination mechanism. It is obvious also that this kind of device is a peculiar 'instrument of gradualness' adapted to reckoning with dynamic spatial and temporal relations between stimuli.

The structural features described here permit us to conclude that already in lower vertebrates the coordination mechanism displays certain aspects peculiar to the analyser-coordination mechanism, though in a still diffuse and little differentiated form, along the whole length of the axial part of the CNS.

It is very probable that the principle of the organization of interneuronal connections in the CNS of lower vertebrates, outlined above, also underlies constructions of the cortical type (see Fig. 19) like the more highly organized structure of the analyser-coordination mechanism, so that they are only a further stage of structural differentiation of the neuronal architectonic relations that appear in the CNS of vertebrates from the moment of its development.

In the evolution of the vertebrates the CNS develops as a complex formation. On the basis of the organization described above it leads to the development of a coordination mechanism with segmental and supra-segmental reflex devices, and also creates the necessary 'organized' prerequisites for subsequent separation of the analysers (the analyser-coordination mechanism, and then the analyser systems) with the forms of switching apparatus characteristic of these formations (and a special construction of cortical type).

5. The Analyser Systems

In the successive articulated chains of neuronal switches that make up the analyser systems (see Fig. 7) are performed those most complex forms of the analytical and synthesizing activity of the brain that ensure the very detailed orientation of the organism in its surroundings. We shall touch briefly on the functional significance of the structural features that distinguish analyser systems from the analyser-coordination mechanism.

The reflex coordinations realized by means of the analyser-coordination mechanism have only limited application in the aggregate of the reflex activity that ensure partial adaptation of the organism to any special complex of stimuli. The basic physiological purpose of this mechanism is to satisfy the growing and increasingly complex coordination requirements of the organism. The analyser-coordination mechanism, in conjunction with the coordination mechanism, is only able to resolve adaptive problems in part, being so to speak an association of neurons with limited physiological responsibility.

With the evolution of analyser systems a sort of self-determination of the analysers comes into being and they take on the quality of a higher superstructure on top of all reflex coordinations. The higher cerebral ends of the analyser systems and their highly complex interconnections, which develop extraordinarily in the course of vertebrate evolution (Fig. 24), process integrated signals from all the receptor fields of the organism. As they become differentiated the analyser systems subordinate the whole aggregate of reflex coordinations of the organism to themselves and utilize them in the interests of the organism as a whole.

Whereas the mechanisms of the axial reflex coordinations are responsible for the physiologically ordered performance of adaptation acts of one kind and another, the higher cerebral ends of the analysers in animals with differentiated analyser systems take over full responsibility for the biological purposiveness of their reactions.

With the development of analyser systems, and especially of their higher cerebral ends, the capacity of the organism to orient itself actively in its surroundings is qualitatively altered, broadened, and deepened, thanks to the improve-

ment in the physiological apparatus for active tuning of the sensory organs to perceive objects. At the same time the organism acquires in turn the possibility of acting in a more and more differentiated way on the objects stimulating it. The analyser systems are a powerful means of not only of adapting the organism to its environment but also of adapting its environment to its needs.

The analyser-coordination mechanism takes on the role, to a certain extent, of 'overseer' of the working of the coordination mechanism, making what corrections are required during its functioning. In fact, this role is restricted to further refinement of the possibilities inherent in the reflex coordinations inherited by descendants from their ancestors; that is particularly clearly marked in those vertebrates whose analyser systems are still poorly developed.

The higher cerebral ends of the analyser systems, in their developed forms (the formations of the fully developed neocortex and of the subcortex contiguous to them—see Figs. 5 and 7), have the most developed functional possibilities of elaborating newer and newer 'artificial' reflex coordinations in the course of an individual life, coordinations that we qualify as habits, skills, and knowledge.

The development of an analyser system as a single, complexly interconnected formation, is particularly clear in the correlation of the processes of structural differentiation of the apparatuses for switching impulses that are located at various levels of the brain. It has been established that the differentiation during intra-uterine life of cyto-architectonic layers in the cortical zones corresponding to the systems of visual, cutaneous, and kinaesthetic analysers coincides with the period of differentiation of the subcortical formations (the thalamus and lateral geniculate body—see Fig. 7) into basic complexes of nuclei (Preobrazhenskaya, 1955; Minaeva, 1961).

Two levels of central switching instances can be distinguished in the analyser systems, corresponding to the axial and supra-axial parts of the CNS. The switches located along the axis can be related to the formations of the lower subcortex, while those located in the transitional region between the axial and supra-axial parts (the thalamus and geniculate bodies), and the subcortical nuclei of the cerebral hemispheres belonging to the supra-axial part, constitute the upper subcortex. The cortical ends of

the analyser systems extend to the limits of the supra-axial part (see Figs. 7 and 29).

It can now be taken as proved that all analyser systems are built on a foundation of two-way connections within the chains of impulse switches forming their intermediate and terminal links, which are represented by the corresponding peripheral, subcortical (forming part of the upper and lower subcortex), and cortical sections. Each link is connected with the others by means both of ascending (centripetal) and of descending (centrifugal) pathways (Rasmussen, 1950; Dzugaeva, 1958; Shkolnik-Yarros, 1958; Kyuypers *et al.*, 1961). Owing to this organization of connections within an analyser system, groups of neurons in the nodes of switches located between its peripheral and higher cerebral ends are constantly under the influence of opposite and mutually interacting streams of impulses. Thus the higher cerebral ends have the possibility of actively influencing in a definite way the functional state of the chains of neuronal switches involved in the transmission of centripetal impulses, stimulating some groups of neurons and at the same time inhibiting others.

The switching instances of the analyser systems that form part both of the axial and of the supra-axial parts of the CNS are closely linked with the coordination and analyser-coordination mechanisms.

By means of the numerous collateral branches leaving the analyser systems along their ascending tracts at the lower levels of the CNS (see Fig. 7), direct contacts are established with the corresponding parts of the other two mechanisms. Thus, through the action of centripetal and centrifugal impulses, the analyser systems can already exert a definite influence in their axial sections on the various reflex coordinations effected by the spinal cord and brain-stem. As a result, the activity of the two mechanisms is changed in the same general direction as the changes brought about in the functional state of the higher cerebral ends of the analyser systems through the effect of these centripetal afferent impulses. In the same way all the reflex adaptations of the organism are alerted in accordance with the reactions and operations performed by the higher cerebral representatives of the analysers in the supra-axial part of the CNS.

The analyser systems can also influence one another

indirectly by way of their connections with the reticular formation in the axial part of the CNS (Fig. 7); but the impulses passing from them to the reticular formation in great measure lose their specific character ('modality'). The new combinations of impulses arising as a result of these interactions can affect the general tonus and working capacity of the higher cerebral ends of the systems via the ascending chains of switches of the reticular formation (the so-called non-specific activating system—see Fig. 17), changing their functional state in the direction either of a raising or of a lowering of the threshold of excitability.

The cortical and subcortical formations located in the supra-axial part of the CNS have extensive two-way (centripetal and centrifugal) connections with many groups of neurons in the axial part (see Figs. 22, 25 and 26); and in these connections, which are specialized to sustain opposite streams of impulses, we are apparently faced with the material apparatus of the complex, directed influences exerted by the higher cerebral ends of the analyser systems (as the integrator of the organism's behaviour as a whole) on the whole aggregate of reflex coordinations.

The development of analyser systems brings about an inner reorganization of the whole neuronal structure of the coordination and analyser-coordination mechanisms as a result of which the higher cerebral ends of the analyser systems are in a state to act selectively in a differentiated way on the effector instruments of the body. Impulses emitted by the supra-axial part of the CNS acquire the possibility of passing to the finest groups of effector elements (the appropriate parts of the skeletal musculature) via the coordination mechanism. Thus, with heightened 'discriminatory' power in the analysers, i.e. as the separate stimuli perceived become more and more divided, the organism begins to react to them with more and more finely differentiated movements. The anatomical basis for that in the CNS is provided by the direct pathway intensively developed in mammals (the so-called pyramidal tract) conveying impulses from the neurons of the motor and other areas of the cortex to the effector neurons of the coordination mechanism (see Fig. 25). This system of centrifugal fibres connecting the cortical zones of the various analysers (primarily the cutaneous and kinaesthetic analysers) with the working reflex apparatuses of the axial part of the CNS

can be regarded as the channel for the fastest passage to the effectors of combinations of impulses programmed in the cortical ends of the analyser systems as a result of their analytical processing and synthesizing of the varied signalization arriving from the perceptive surfaces of the organism (see Chapter II, section 7).

The findings of comparative anatomy and physiology give grounds for supposing that the complexes of neurons making up the coordination mechanism began, with the development of analyser systems during the evolution of mammals, to work on two parallel planes, as it were, on the phylogenetically older one of ensuring vitally important adaptive reflex coordinations and on the phylogenetically younger one of specially sustaining reactions established and brought about mainly by means of the analyser systems. This functional division of the coordination mechanism is reinforced morphologically in the various systems of centripetal and centrifugal connections that link the corresponding groups of neurons of this section of the CNS with the higher cerebral ends of the analyser systems.

The neuron complexes of the coordination mechanism formed in the relatively early stages of evolution, prior to the formation of the analyser systems, preserve an essential function, even in the more highly developed vertebrates, of conveying recepts of vital importance to the organism to the higher cerebral ends of the analyser systems. What we have in mind are the recepts evoked by signals coming from the internal medium of the organism and carrying information about the intimate processes of biological activity and recepts elicited by pain stimuli from the damaged tissues of the body. This type of recepts, which is associated with global defensive and vegetative reactions, belongs to the category of coarse or protopathic sensibility, in contrast to the finely differentiated discriminatory or epicritical sensibility inherent in the analyser systems.

The chains of neuron switches along which impulses of protopathic sensibility reach the supra-axial part of the CNS are localized (as has been established by recent research) in definite sections of the reticular formation very closely linked with the group of phylogenetically ancient nuclei in the thalamus that form part of the cephalic subcortex. These formations are connected in turn by two-way

pathways with many regions of the cerebral cortex. Particularly numerous are the connections established in this way with the older (in evolution) formations of a cortical type (the palaeo-, archi- and intermediate cortex in Filimonov's classification), and with those areas of the neocortex that are differentiated earlier in the evolution of mammals, i.e. the marginal (limbic and insular) regions of the neocortex and those of its formations occupying the medial and basal surfaces of the hemispheres in the frontal and temporal lobes (see Figs. 22, 46 and Plate V).

These systems for circulating impulses between the cerebral cortex and the corresponding sections of the reticular formation of the brain-stem and the between-brain thus ensure integration of the animal and vegetative components of reactions to vitally important stimuli. Further details of the physiological importance of these various forms of connection between the axial and supra-axial parts of the CNS will be introduced in the next chapter.

The complication in the course of evolution of the whole organization of switches uniting the axial and supra-axial parts of the CNS has resulted in components of reflex activity, which are at once different in their functional significance but interrelated, and which are located in the lower levels of the brain and spinal cord, being represented in the higher cortical ends of the analyser systems. In the constellations of neurons that form the cerebral cortex various forms of interaction with the corresponding parts of the coordination mechanism are combined in a complicated functional and topographical pattern. All vertebrates retain chains of neuron switches adapted to exert a general tonic, 'dynamogenic' influence of a generalized character and closely linked with protopathic recepts. In addition, in the higher vertebrates (mammals), apparatuses of intercentral interaction come more and more to the fore and are more strictly localized and related to separate groups of cortical and sub-cortical neurons; by means of them finely articulated, selectively directed, differentiated reactions conditioned by epicritical recepts are effected.

As confirmation of this conception of the functional connections between the 'specific' and 'non-specific' components of the systems of links between the cortex and lower sections of the CNS we would cite the following. Decorticated animals have been shown to be incapable of

performing local, conditioned motor acts, i.e. acts limited to very definite muscles, although retaining general motor reactions like running to food.

The complex systemic character of functional localization in the CNS is the key to understanding the most essential aspects of its organization. Such a conception brings us close to an answer to the problem of how the separation and unity of the animal and vegetative functions are realized, and how fine discrimination is achieved between separate stimuli and between the responses to them, as well as global reactions to gross or acute external influences on the organism. On this foundation are built up the lower and higher levels of integration of reflex acts of varying complexity, based on the interconnection of differently specialized complexes of neurons.

CHAPTER II

REGULATION, CONTROL, AND DIRECTION IN THE ANIMAL ORGANISM

1. The Problem

So far as we know there is no precise definition of what is concretely understood by the regulation, control, and direction of biological systems. The concepts are often confused, or used as synonyms.

Yet all the latest advances in the designing and practical utilization of various cybernetic systems are based, in the final analysis, of course, on the principle of modelling the laws of living nature. One of the most fruitful lines of development will probably be deeper and deeper study of biological structures and experimental reproduction of the principles underlying them. The birth of new disciplines like bionics and neurocybernetics in our time can be taken as obvious confirmation of this view which holds out unlimited possibilities for building still more perfected systems.

Basing ourselves on these considerations we first endeavoured to formulate the concepts of **'regulation'**, **'control'**, and **'direction'** in a broad sense, i.e. to embrace **'auto-regulation'**, **'auto-control'** and **'auto-direction'** and to give them concrete definitions based on analysis of biological objects. Behind our reasoning were the data analysed in Chapter I on the evolution of the neuronal organization of the brain. We consider that the interaction of the functions with which we are concerned here embraces all manifestations of reflex activity from the simplest to the most complex. On the other hand, however, we are deeply convinced that the biological and physiological significance

of this activity at all stages of evolution can only be adequately expressed by these concepts.

Reflexes embrace processes of varying complexity and biological significance governed by the general laws of development of self-organizing systems. Each class of reflex adaptations is realized through definite morphological and physiological mechanisms located at various levels of the CNS. Our object in this chapter (as in the preceding one) is to present a differentiated picture of the structural and functional organizational features of the mechanisms involved, and of their interrelations.

In our essay at giving a rational explanation of the significance of these various reflex mechanisms, according to their level of development, we take as our starting point the principle that the regular functioning of a system capable of signalling activity is determined by an adequate relationship between a certain degree of centralization and local autonomy in definite sections of the neuronal organization. In order to elaborate our view we must touch on the general problem of functional localization in the brain, and to trace the way it has developed in complexity in the course of evolution.

2. The Functional Significance and Interconnections of Reflex Mechanisms of Different Levels of Organization

Let us now consider certain important features of the functional architecture of the three basic sectors of neuronal organization outlined in Chapter I and their significance in regulation, control and direction. We shall link these functions with the three successive stages of progressive complication of neuronal organization.

It is a basic tenet of Pavlovian theory that all reflexes can be divided primarily into two major spheres of phenomena—species (unconditioned-reflex) and individual (conditioned-reflex) adaptations. The evolutionary accumulation of species experience is fixed in reactions of various degrees of complexity performed at various levels of the CNS, beginning at the spinal cord and finishing at the phylogenetically older subcortical and cortical formations of the cerebrum. And these reactions are subordinated to relatively stable, but slowly changing, programmes gradu-

ally elaborated during the long evolution of species. This group of reflex adaptations, fixed in a certain configuration of nerve connections, can be assigned to the independent class of self-organizing functional systems that we group together as the aggregate of auto-regulatory, auto-controlling, and auto-directional processes.

From the neurophysiological aspect these functions can be pictured as follows. Auto-regulation (as we understand it) is a complex of relatively elementary animal reflex acts of a predominantly local character, and of various vegetative reactions. Auto-control we regard as a complex of more complicated adaptational animal reactions (plus their vegetative components) that link together the different systems of local reflexes. The function of auto-direction embraces the most complex innate (instinctive) forms of behaviour directed to satisfying the biological needs of the organism. The whole aggregate of these functions (which can be characterized as a hierarchy of unconditioned-reflex connections) is thus the means by which the forms of species experience of various levels of organization are realized.

The essence of unconditioned reflexes of whatever degree of complexity that provide the necessary basis for the accumulation of living experience is that they are relatively independent of individually acquired conditioned reflexes. All manifestations of the latter, from the simplest to the most complex, we assign to a single, common group of regulatory, control, and directive processes. The leading role in this is taken by direction (by means of which the most complicated, variable forms of behaviour are effected), but control and regulation (as will be shown in the following sections) also have important auxiliary functions in the mechanisms both of direction and of auto-direction. Through them the interaction of individual and species experience is accomplished, as a result of which the organism's innate activities are adapted to the special conditions of its environment.

Thus, from a concrete analysis of the evolved complexity of brain structure, comparing the known physiological data, we distinguish auto-regulation, auto-control and auto-direction as special forms, in addition to regulation, control, and direction in the narrow sense, and relate each of these functions to a definite, topographically delimited, anatomical and physiological mechanism.

Further, with both auto-regulation and regulation in mind, we group these concepts under the single common term of auto/regulation; similarly, for auto-control and control we use the term auto/control, and for auto-direction and direction that of auto/direction.

The biological principle and physiological mechanism of auto-regulation undoubtedly underlies living phenomena. Auto-regulation is the basis on which the living system arises and exists with all its physiological adaptations. Plants are in essence a natural auto-regulating system, the adaptive potentials of which do not extend beyond the limits of the function.

Animals, in contrast, are capable of perceiving and processing information about events occurring in their external environment and inside them, and of transforming it into activity of the organism. They possess a corresponding material organization in the form of an apparatus of nervous signalling that does not exist in plants. Thus property of auto-regulation possessed by all living creatures is transformed in them into special forms of auto-regulatory processes effected by means of a nervous system.

One of the principal features distinguishing the animal way of life from the vegetative is that the reflex life of animals is not, therefore, restricted to processes of auto-regulation (performed, as we have said, by means of nervous signalization). On the basis of the signal activity developed (which is initially capable only of elementary auto-regulation of biologically important functions), mechanisms of regulation, auto/control, and auto/direction are subsequently built up. Thus, whereas plants can be characterized on the whole as auto-regulating biological systems, animals are, in addition, regulated, auto/controlled, and auto/directed systems. That means that an animal, as a biological system, possesses behaviour. The highly developed animal organism is a most complex interweaving of interconnected mechanisms of auto/regulation, auto/control, and auto/direction.

The development of analysers came about mainly through the appearance of new biological needs of the organism that went beyond the limits of auto-regulating reflex adaptations; and that determined the whole growing role of regulation, auto/control, and auto/direction in the organism's adaptive reactions. The development of all these functions,

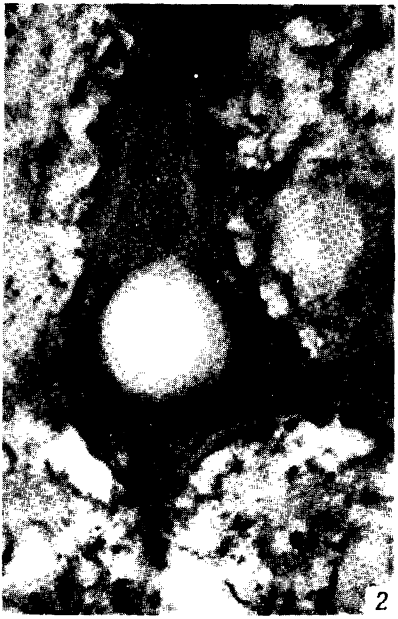


Plate III. Terminal contacts formed by axons with cortical neurons. *1*, pin-shaped terminal contacts with giant Betz cells (after Poliakov, 1955); *2*, end buttons on the body and initial sections of the dendrites of a pyramidal cell; *3*, the same on stellate cell (preparations by Blinova).

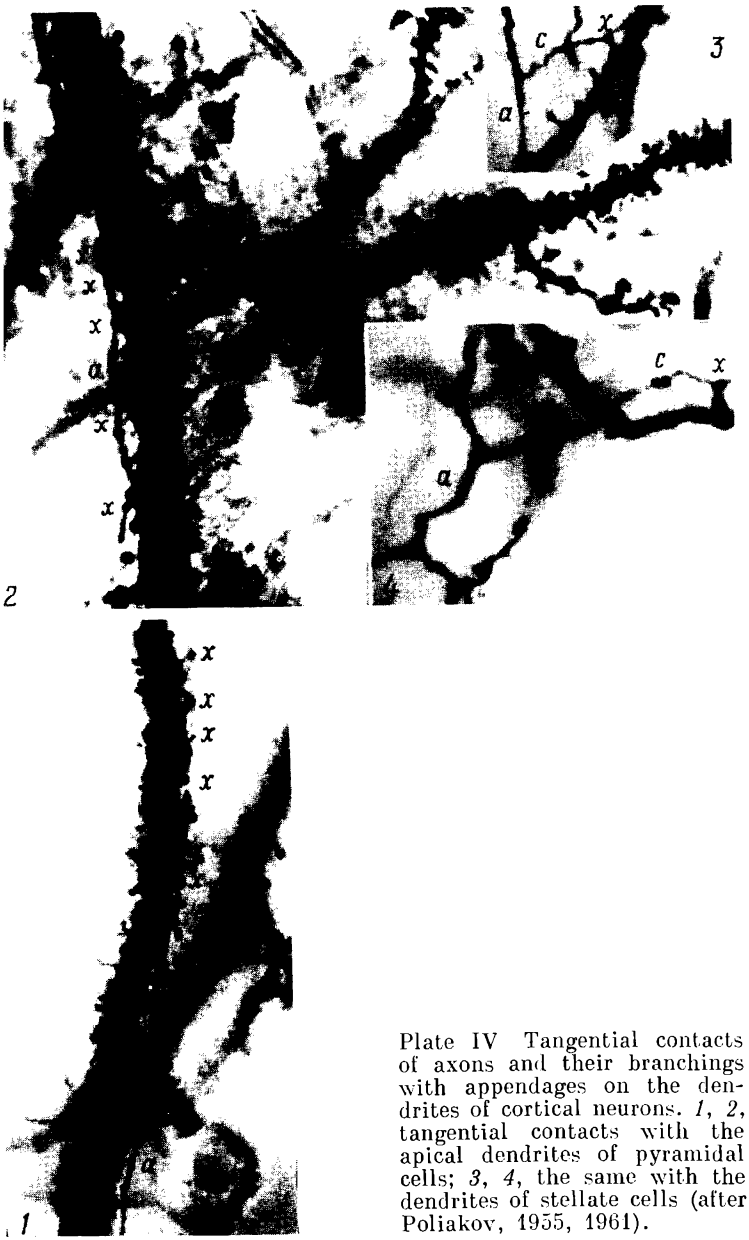


Plate IV Tangential contacts of axons and their branchings with appendages on the dendrites of cortical neurons. *1*, *2*, tangential contacts with the apical dendrites of pyramidal cells; *3*, *4*, the same with the dendrites of stellate cells (after Poliakov, 1955, 1961).

above all of auto/direction with its relatively more complexly organized nervous substratum, was seemingly brought about by the fact that adaptation to the external environment has a complexly mediated character. in moving creatures possessing signalling activity and capable of active orientation. An animal has to have the ability not only to accumulate past experience but also to 'anticipate' events, unlike plants, which are in a position only to adapt passively ('retrospectively') to the changes taking place around them. The very need of active means of interacting with the environment led to the formation in animal organisms of more complex functions built up on elementary processes of auto-regulation of the biological activity of the body.

In its most general form auto-control can be characterized as a transitional stage between auto-regulation on the one hand and auto-direction and direction on the other. Under auto-control we also understand the lower stage preceding the appearance of developed auto-direction and direction, when these functions have still not developed sufficiently to dominate the vital (mainly animal) auto-regulations in the interest of the organism as a whole. In other words, at the stage of auto-control these functions are only able to manifest themselves in partial, limited forms through which a more developed organization of some combination or other of the organism's auto-regulating systems is achieved. Consequently the mechanism of auto-regulation developed earliest of all in the evolution of the animal kingdom and then that of auto-control, while the mechanisms of auto/direction took shape much later (Fig. 5).

Lyapunov (1963) has made an analysis on the plane of cybernetics of the phylogenetic and ontogenetic complication of the interrelations of functions of different levels of organization involved in the organism's reactive activity. As the basis for objective systematization of these functions he took the interactions of control systems of various levels. The evolution of living nature is characterized as a process of proliferation and selection of control systems. Lyapunov also seems to understand these different levels of control as a combination of processes of auto/regulation, auto/control, and auto/direction in our use of the terms.

The assumption that the same effector instruments, the

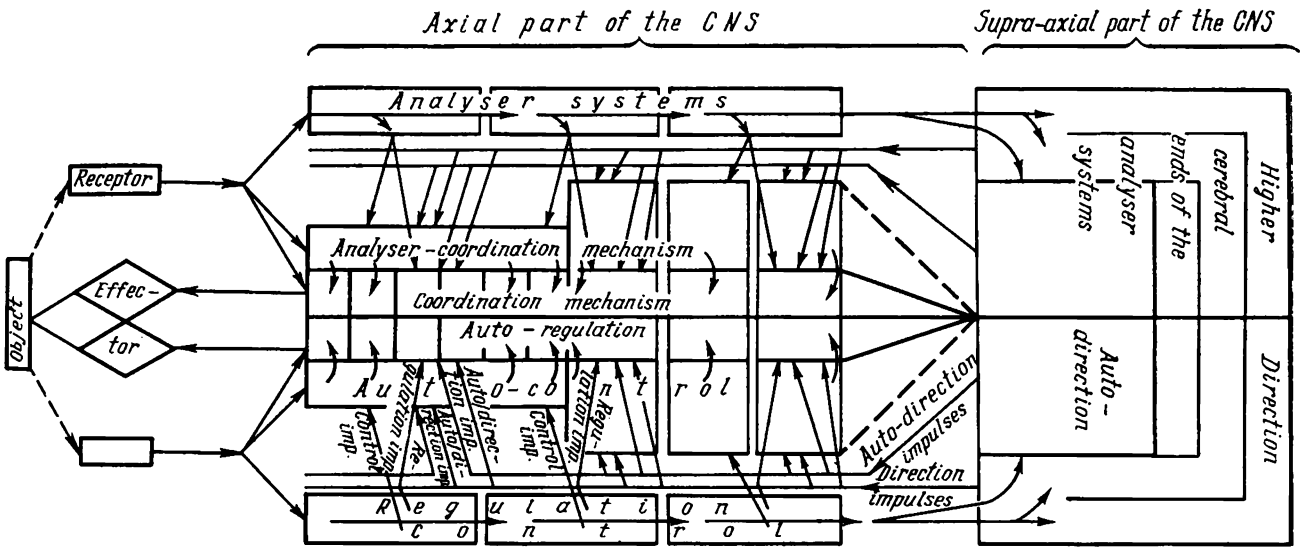
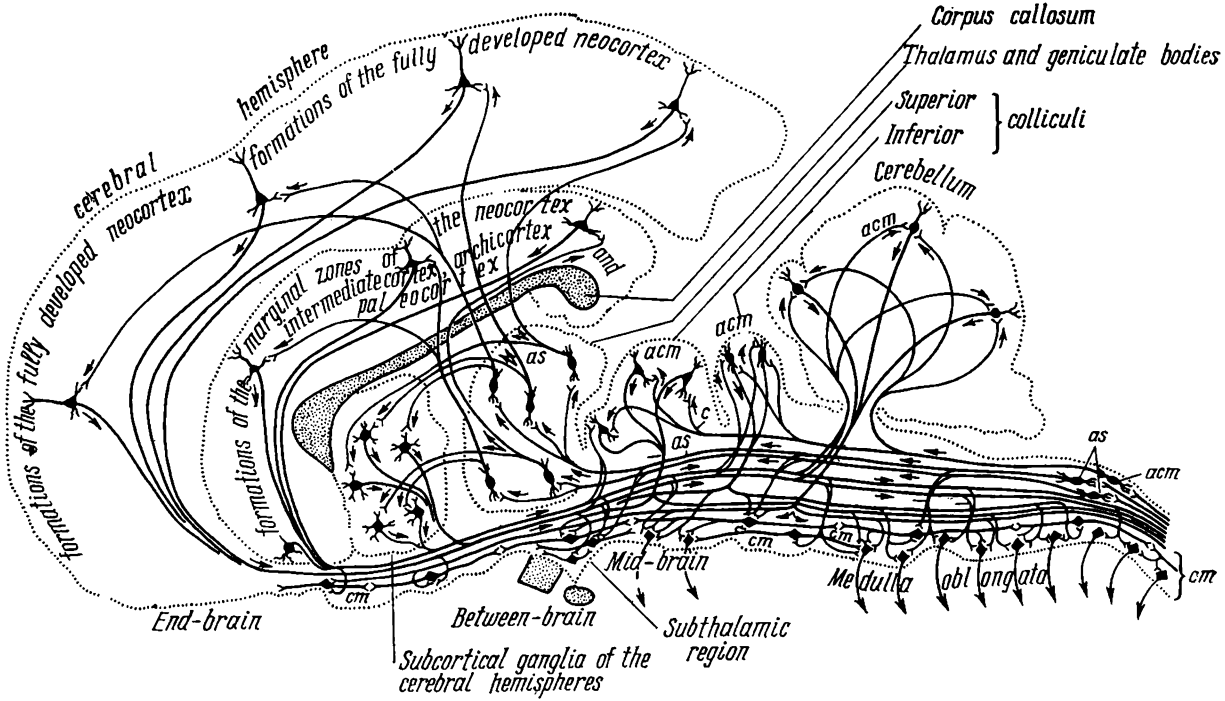
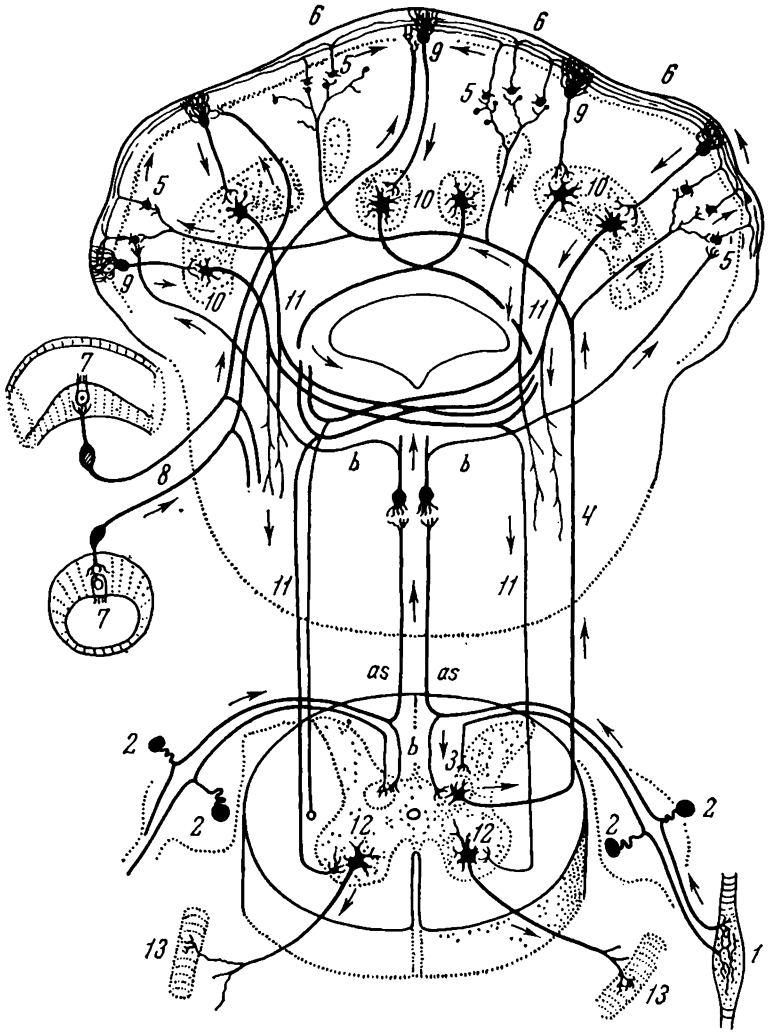


Fig. 21. Block diagram showing the interrelations of the different sections of neuronal organization (see the left-hand side of the diagram), and the functions of auto/regulation, auto/control, and auto/direction (see the right-hand side). To simplify the diagram, the centrifugal connections in the analyser systems have not been represented.



F i g. 2 2. Schematic diagram of the anatomical relations and connections between the central nervous formations by which the functions of auto/regulation, auto/control, and auto/direction are realized; *as*, analyser systems; *acm*, analyser-coordination mechanism; *cm*, coordination mechanism.



F i g. 2 3. Diagram of the neuronal switches and connections in the cerebellum; *1*, receptor ending of a sensory nerve fibre in striped muscle; *2*, peripheral sensory neuron in a spinal ganglion; *3*, switching nucleus in the spinal cord, projecting into the cerebellum; *4*, centri-

terminal executive links of reflex arcs and analysers, effect the most varied reflex acts involving different degrees of auto/regulation, auto/control, and auto/direction is of vital importance in explaining the basic pattern of functional localization in the CNS.

Analysis and synthesis of stimulation are necessary preconditions of ordered reflex activity at any stage of its phylogenetic elaboration, and are manifested differently depending on the relations between their development. At the lower levels of development of the analysers represented by the analyser-coordination mechanism the results of analysis and synthesis of stimulation are utilized (as will be shown below) for auto-control, and at higher levels for functions of regulation, control, auto-direction, and direction.

We relate auto-regulation and auto-control (see Figs. 21 and 22) to the reflex coordinations of the axial part of the centralized nervous system; auto-regulation we assign to the coordination mechanism, and auto-control to the analyser-coordination mechanism. Auto-direction we relate to the phylogenetically older and less organized cortical sections of the higher cerebral ends of the analyser systems located in the supra-axial part of the CNS (i.e. to the formations of the palaeo-, archi- and intermediate cortex—see Fig. 22) and the subcortical formations adjoi-

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petal pathways from the spinal cord to the cerebellum; *5*, switching elements (grain cells) in the cerebellar cortex; *6*, horizontal bundles formed by the fibres of these neurons and establishing contacts with the efferent neurons (Purkinje's cells) of the cerebellar cortex (9); *7*, receptors of the organ of equilibrium (vestibular and otolithic apparatus of the inner ear); *8*, centripetal pathways from the organ of equilibrium to the cerebellum; *9*, efferent neurons of the cerebellar cortex (Purkinje's cells), emitting impulses directed to the reflex centres of the skeletal musculature; *10*, switching nuclei in the pathways of these impulses located under the cerebellar cortex; *11*, conducting pathways of centrifugal impulses from the cerebellum to the spinal cord; *12*, effector neurons of the spinal cord innervating striped muscle; *13*, motor nerve endings in muscle; *as*, analyser systems; *b*, branchings from the analyser systems to the switching nodes forming part of the cerebellar connections (after Ramon y Cajal, with certain modifications).

ning to them, that is to say, to the structures of the brain that constitute in aggregate the morphological and physiological foundation of innate forms of behaviour (see sections 5 and 6 of this chapter).

In our conception the higher ends of the analyser systems (represented by the phylogenetically newer and more highly organized cortical formations of the cerebrum, i.e. the formations of the fully developed neocortex—see Figs. 22, 24, 46 and Plate V; plus their adjacent subcortex—see Figs. 7 and 29) perform the most responsible function of direction, which is realized through the influence they exert both on the older cortical and subcortical formations of the supra-axial part of the CNS that constitute the anatomical and physiological basis of auto-direction and on the reflex-coordination mechanisms of the axial part.

Regulation and control are effected through the mediation of the connections established between the coordination and analyser-coordination mechanisms and the switching stations of analyser systems located along the axial part of the CNS (see Figs. 7 and 23) (regulation in relation to the coordination mechanism and control in respect of the analyser-coordination mechanism).

This scheme of interconnections between auto/regulation, auto/control, and auto/direction agrees with Wiener's idea (1961) that the functioning of self-organizing systems is built up on the interaction of subsidiary algorithms of various levels. The algorithms characterizing each of these levels ensure the definite forms of processing of information required to realize the system's purposive behavioural acts. The highest level is related to the elaboration of 'self-learning algorithms'

Thanks to the combination of the principles of relative autonomy and centralism in the functioning of reflex mechanisms, forms of subordination are ensured such that lower instances can carry out their special functions without involving central nervous formations located higher up the hierarchical ladder. At the same time the latter are freed from any need to participate directly in the current 'everyday' work of the lower reflex apparatuses. The higher instances, however, do preserve their potential for constant and active interference in the activity of the lower ones, thus altering its direction and character in accordance with changes in the external situation and the estab-

lished behavioural programmes. Examples of this kind of interaction will be considered in the appropriate sections of this chapter.

From our short survey of functional localization as applied to the various sections of neuronal organization it follows that the reflex coordinations of the axial part of the CNS, taken together, can be characterized as a complex aggregate of auto-regulating and auto-controlling devices that are in turn under constant influences of regulation, control, auto-direction, and direction. In organisms with undamaged brains these reflex coordinations can be likened to performers obeying signals of auto/direction and their accompanying signals of regulation and control. The supra-axial part of the CNS (see Fig. 2), having achieved the highest degree of centralization, has at its command the entire reflex resources of the organism, being the most perfected tool by means of which the behaviour of the whole organism is determined and directed.

In the higher cerebral ends of the analyser systems that form this part of the CNS and are connected with the most complex forms of analysis and synthesis of stimulation, behavioural patterns are built up from the organism's vitally important biological needs. These patterns presuppose the reproduction of adequate models of the external world in the brain in the form of images and concepts of concrete objects for satisfying needs; with these models also are linked the programmes elaborated during the course of the accumulation of individual experience that underlie the operations to be performed ('motor tasks' as Bernstein terms them).

The transition from the axial part of the CNS to its supra-axial part, which anatomically coincides with the boundary between the mid-brain and the between-brain (see Figs. 2 and 7), is the junction between the apparatuses responsible for auto/regulation and auto/control on the one hand, and auto/direction on the other.

In invertebrates auto-regulation (the coordination mechanism) is the function, seemingly, of the thoracic chain of ganglia (see Fig. 2); auto-control (the rudimentary analyser-coordination mechanism) can be thought of as linked with the head sub-glottal ganglia, while the function of auto-direction (the elementary systems of analysers, which in these animals are predominantly specialized to fix species

experience) belongs to the supra-glottal ganglia of the head.

The distribution and character of the interaction of auto/regulation, auto/control, and auto/direction in the aggregate of reflex activity depend on the relationship in development of the coordination mechanism, the analyser-coordination mechanism, and the analyser systems. The analysers, performing functions mainly of regulation, auto/control, and auto/direction, are the material substratum of the more complex forms (predominantly linked with the animal reflex sphere) of central processing external signals relating the organism to its environment; only a relatively insignificant part of external signalling is addressed directly to the auto-regulatory apparatus of the coordination mechanism. On the contrary, central processing of signals concerned with the vegetative reflex sphere, and coming from receptive surfaces in the internal medium, is mainly the function of the coordination mechanism and is utilized for auto-regulation of the internal biological activity of the body.

The principle of feed-back, which is of universal importance in reflex activity of all levels of complexity, is realized in different ways in the functions of auto/regulation, auto/control, and auto/direction. The algorithms of reflex coordinations are directly fixed in the auto-regulatory and auto-controlling apparatuses of the coordination and analyser-coordination mechanisms; and through the corresponding organization of interneuronal connections (see Figs. 11 and 16), a central apparatus is provided for comparing, correlating, and evaluating the reactions actually performed with what was programmed. The actions are corrected naturally during their performance by the deviation of their separate components from the limits of the physiological parameters allowed for the auto-regulatory and auto-controlling systems concerned. Thus, for example, a most essential condition ensuring coordinated performance of any reflex motor act is in Bernstein's view the overcoming of excess degrees of freedom in the moving organ by means of sensory corrections by which the movement is given a dynamically stable character, i.e. becomes auto/regulated, auto/controlled, and auto/directed.

The central apparatuses for correlating the end result of reactions with their programme are localized at all levels

of the CNS. The main components of this activity are linked with the sections of neuronal organization that perform the functions of auto-direction and direction. Bernstein's research into motor coordinations has convincingly shown that the corrections required during performance of the consecutive stages of an operation are effected by the switching formations of the analyser systems located at various levels of the CNS. In that way afferent syntheses of varying degrees of complexity are built up, and the switched impulses directing the flow of the appropriate components of an integrated motor act are recoded.

3. Auto-regulation and Regulation

As already noted in section 3 of Chapter 1, the auto-regulating devices of the organism include the more elementary and ancient physiological processes (ancient as regards both their phylogenetic origin and their ontogenetic development) by means of which the definite reflex adaptations formed during the evolution of the animal species concerned are preserved in a stable and constant form. Apart from the auto-regulations of the different vital functions of the body performed by the vegetative nervous system (see Fig. 13), individual components of statics and locomotion, primitive defensive, adaptational, and feeding reflexes from the sphere of animal life must be included in this group. All similar types of auto-regulation, of course, belong to the category of involuntary, unconscious reflex acts, i.e. not subordinated to conscious, voluntary direction. From the anatomical and physiological aspect they are subject to the jurisdiction of local segmentary reflex arcs, which, along with the suprasegmentary apparatus uniting them, make up the coordination mechanism.

Any reflex coordination belonging to the coordination mechanism is, in our view, a definite auto-regulation apparatus arising from the experience of generations. The coordination mechanism as a whole, with its segmentary and suprasegmentary sections, constitutes the anatomical and physiological base of the oldest auto-regulating reflex adaptations of the organism.

All local segmentary reflexes are completed, as we know, on the principle of conjugate, functional agonist-antagonist pairs (see Fig. 11). The agonist and antagonist can, conse-

quently, be looked upon as two conjugate members of an elementary, biological, auto-regulating system, the constitutional features of which ensure automatic balancing out of deviations from the normal physiological standards of the system. It is this principle of reciprocal innervation, which is present from the very rise of the auto-regulating animal system, that underlies (as we have indicated) ordered reflex activity.

Taking into consideration Orbeli's research (1962) into the role of the cerebellum in the adaptational, trophic processes linked with the sympathetic nervous system, it can be supposed that some vegetative auto-regulations involve a certain degree of auto-control, i.e. depend on the analyser-coordination mechanism.

By regulation, in contrast to auto-regulation, is understood a physiological device located in the axial sections of the analyser systems, by means of which auto-regulatory adaptations effected by the coordination mechanism are finely correlated with reflex activities that are determined by the organism's general orientation in the world around it and have their material basis in the analyser systems and their connections with the coordination mechanism.

Among the morphological components concerned with regulation are, we think, the numerous collateral branchings noted above that pass along the axial part of the CNS to the segmental and suprasegmental formations of the coordination mechanism, and that begin in the switching nodes and bundles of centripetal fibres forming part of the analyser systems (see Fig. 7). The collateral branches to which we refer run both to neurons of the reticular formation and to effector (motor) neurons of the spinal and brainstem parts of the brain.

The flow of impulses running to the higher (supra-axial) cerebral ends of the analyser systems, and transformed there into impulses of auto/direction, can simultaneously effect all the auto-regulatory physiological systems of the organism by way of these interneuronal connections. Because neurons linked with the coordination mechanism and forming part of the switching nodes located in the axial sections of the analysers, come under the permanent influence not only of centripetal impulses but also of centrifugal ones, the latter can also change the state of the coordination mechanism in one direction or another. Thus ad-

ditional premises are created for opportune mobilization of all the reflex forces of the organism in connection with its external activity directed to accomplishing definite biological aims.

Obviously the weaker the development of the analyser systems as a whole the less marked their regulatory influence on the working of the coordination mechanism will be, and the more that 'free' auto-regulations (i.e. not subordinated to auto/direction) will come to the fore in animal reactions (see section 9 of this chapter).

From the foregoing it will be clear what an important, auxiliary role regulation has in the functions of auto/direction.

4. Auto-control and Control

The basic physiological purpose of auto-control is to ensure complex interaction between the various auto-regulations of the organism in accordance with its active orientation in the external world, which finds its 'organizational-morphological' expression in the analyser-coordination mechanism. Unlike the coordination mechanism the latter embraces more complicated combinations of auto-regulatory systems and raises the adaptive potential of the organism in respect of a wider round of changes in its environment.

The reflex coordinations tied in with the analyser-coordination mechanism are complex unions of auto-regulating reflex adaptations (which also occur automatically and involuntarily) predominantly concerned with the animal existence of the organism. Their orderly flow requires 'inspection', and that in fact is the role of auto-control; they could, therefore, be defined as auto-controlling auto-regulations.

The qualitative complication of auto-controlling adaptations in contrast to simple auto-regulating ones consists in the following: an auto-regulating apparatus is concerned with a relatively narrow round of physiological parameters, strictly determining its working regime and not exceeding the limits of conditions directly linked with the character of the activity performed; in contrast, the auto-controlling apparatus already represents a more or less complex physiological aggregate of auto-regulating systems and in its operation to some extent takes into account changes occurring beyond immediate sphere of influence and affecting one or other of the auto-regulating systems that make it up.

The auto-control function unifies the various static and locomotor reflexes, reflexes that maintain the static and locomotor equilibrium of the body, and that are closed through the vestibular apparatus, the cerebellum, the visual analyser, and recepts from the whole skeletal musculature and the skin. This category of reflex coordination, which involves auto-control, also includes the various orienting reflexes effected through the lower cerebral parts of the analysers, adaptation reflexes of a certain degree of complexity, and the self-tuning reflexes of the analysers to stimulation (for example, the interaction of various forms of muscular tonus, and the changes in the diameter of the pupil of the eye in accommodation and convergence).

The cerebellum with its highly developed connections (see Fig. 23) and the switching nodes of the brain-stem subordinated to it can be likened to a much improved auto-controlling apparatus ensuring normal performance of various reflex coordinations on the scale of the organism as a whole. This automatically and unconsciously functioning 'supreme organ' of auto-control integrates the activity of several physiological systems, viz. the skeletal musculature, the organs of equilibrium (the vestibular and otolithic apparatus) and visual recepts and unites them for joint functioning in accordance with signals of auto/direction coming from the higher ends of the analyser systems (see Fig. 26). The visual lobes of lower vertebrates (see Fig. 6) are also important correlation centres by means of which complex coordinations of motor acts are realized on the basis of functional unification of indications from various sensory organs.

The basic field of auto-control, like that of auto-regulation, is that of reflex adaptations established during the life of the whole species. But auto-control depends in greater measure than auto-regulation on the function of auto/direction. The grounds for our conclusion are that the most complex inborn reflex adaptations (static and locomotor, for example) effected through the cerebellum require initial training not only in man but also in many animals. The close functional interconnection between the lower and higher parts of the analysers is expressed in a similar kind of anatomical and physiological correlation.

The physiological mechanism of auto-control, like that of auto-regulation, possesses a high degree of autonomy

in respect of higher instances of the brain. Evidence of the relative functional independence of both from the analyser systems, and especially from their higher, supra-axial sections, can be seen in the following. A cat whose cerebral hemispheres have been removed can perform a number of complex motor reflex coordinations, and can run, jump, even climb a tree. At the same time, such an animal as a result of loss of impulses of auto/direction quite loses any biological aims. It is incapable of altering its behaviour in a purposeful way, that is, to ensure that the state and activity of its organism are adequate to the situations occurring around it. In essence, it is really reduced to a 'living reflex automaton' that retains the possibility of performing even quite complicated coordinations but has lost forever the capacity to receive and utilize 'meaningful' information about events.

Animals with the highest, most frontally located (supra-axial) part of the brain removed remind one in some ways of a marionette that moves only when the strings are pulled. Although the reflex responses induced by appropriate stimuli have a quite orderly character, they are not, however, integrated into a single whole and do not constitute behaviour.

We draw the distinction between auto-control and control on the basis of the same general anatomical and physiological premises as distinguish auto-regulation from regulation.

As we have already said, we consider the physiological mechanism of control over the functioning of auto-controlling apparatuses to be an important link in individually established adaptations. We relate this mechanism to the axial sectors of the analyser systems; one of its morphological components is the connection established in the course of evolution between the lower (spinal and brain-stem) switching instances of these systems and the analyser-coordination formations located along the axial part of the CNS (Fig. 23*b*). By means of influences transmitted across these connections, the streams of signals spreading through the switching nodes in the analyser systems alter the functional state of the analyser-coordination mechanism in accordance with changes taking place in the higher ends of these systems under the action of the same impulses. Because there are pathways in the analyser systems (in

addition to those conducting centripetal impulses) that conduct impulses in a centrifugal direction the apparatuses of regulation and control can take into account (in influencing auto-regulating and auto-controlling devices) not only the character of the stimuli but also the state of the higher sections of the brain.

Depending on the character of the ensuing reactions—their direction, duration, and intensity—impulses of regulation and control spreading in the axial sectors of the analyser systems bring about shift in the activity of the corresponding auto-regulatory and auto-controlling systems of the organism from one level to another. These functional shifts, strictly speaking, also include the subsidiary significance possessed by the regulating and controlling apparatuses in carrying out commands of auto/direction coming from the higher sectors of the CNS that cannot be fully realized without these supplementary functions.

5. General Character of Auto-direction and Direction

Auto-direction and direction can be likened to two closely interconnected functions of an originally single cerebral organ. Their importance for the organism is determined by the fact that the built-in structural potentials of the instruments of auto-regulation and auto-control are themselves inadequate to cope with the complicated problems that arise for higher-developed creatures during their active everyday adaptation to changing environmental conditions and during their adaptation of the environment itself to their requirements. Solution of these problems presupposes, above all, determination of the biological significance of the agents acting on the organism, and the purposive utilization of reactions of one sort or another, whether innate or established during life. Thus all the auto-regulatory and auto-controlling reflex adaptations of any organism are correlated with the results of its general orientation in its surroundings and with evaluation of the signal content of the events occurring there.

As already noted, auto-direction and direction, in contrast to auto-regulation and auto-control, are concerned with the most complexly differentiated phenomena of reflex activity. Their anatomical substrata are the higher ends

of the analyser systems intensively developed from the end-brain during the evolution of vertebrates. The formations of the end-brain (which, in the more highly developed vertebrates, are the cerebral hemispheres and their cortical and subcortical formations—see Fig. 22) are decisive for the integration of complete acts of behaviour, being physiologically (in Pavlov's definition) the organ of higher nervous activity.

According to the findings of Asratian, Airapetyants (1960), and others, the cerebral cortex plays a leading role in the organization of defensive and adaptational activities directed to compensating disrupted functions localized in lower parts of the CNS. The triggering of the reflex coordinations preserved in the system of newly established conditioned-reflex associations that enables defects to be compensated is ensured by cortical influences; and as a result new coordinations are formed in place of those lost. In decorticated animals the range of the adaptive and compensatory potential of the organism is drastically reduced.

Being related to the most complex forms of analysis and synthesis of stimulation, and ensuring the fullest orientation in the external world, the higher ends of the analyser systems are a perfect instrument enabling the organism to anticipate events on the basis of past experience and to direct its acts accordingly. The formations of the end-brain of which we are speaking are the true organizer of all behaviour. That important aspect of higher nervous activity is realized as a function of direction in the widest sense of the term, i.e. as auto/direction. In Ashby's definition (1963) rational activity amounts in the final analysis to processes of direction.

Being the cerebral organ for resolving the tactical and strategic tasks of behaviour the apparatus of auto/direction effects a choice and programming of reactions, actions and operations performed in a definite sequence.

'Refusal' of the function of auto/direction is most characteristic in precisely those situations where a choice cannot be made for one reason or another between several possible solutions to a problem. As Ashby remarks, inappropriate behaviour is observed in such conditions. A chaffinch for example, when torn between two contradictory drives—fear of the feeding-dish and desire to reach the

food in it—may often behave in a very strange way and begin to preen its feathers.

Auto/direction is the final, completed stage of the analytical processing and synthesizing of all the signals being received by the higher ends of the analyser systems both from outside and from within the organism. In this series of processes we see a natural expression of the general law that any organized system capable of auto/direction presupposes, as a necessary precondition, the receiving of all-round information about all the conditions of its existence in the world around it.

Concretely, we understand by auto/direction the capacity of the organism selectively to switch on or amplify certain reflex coordinations, and to switch off or moderate others in accordance with the external situation; to carry out a variety of switchings from one coordination to another, and to change the direction of their action and the character of the interactions.

In the phylogenesis of the animal kingdom the apparatuses of auto/direction become progressively more important and acquire a more and more complexly differentiated character as the functions of auto-regulation and auto-control become more and more specialized. A manifestation of this law is the fact that the more highly organized representatives of the invertebrates (crustaceans and insects) display a greater incapacity to orientate themselves in the external world and more marked behavioural disturbances when their brains have been removed than do lower animals like worms. The difference in the symptoms of loss of stimuli of auto/direction is even more striking in vertebrates according to the level of organization of the higher sections of the brain.

On the whole the interactions and interconnection of the functions of auto/direction are determined by the whole concatenation of innate and learned components of behaviour characteristic of a representative of a given animal species.

6. Auto-direction ('Unfree' or Automatic Direction)

By auto-direction, which may also be characterized as 'unfree' or automatic direction, and which is a phylogenetically older level of development of the mechanisms of

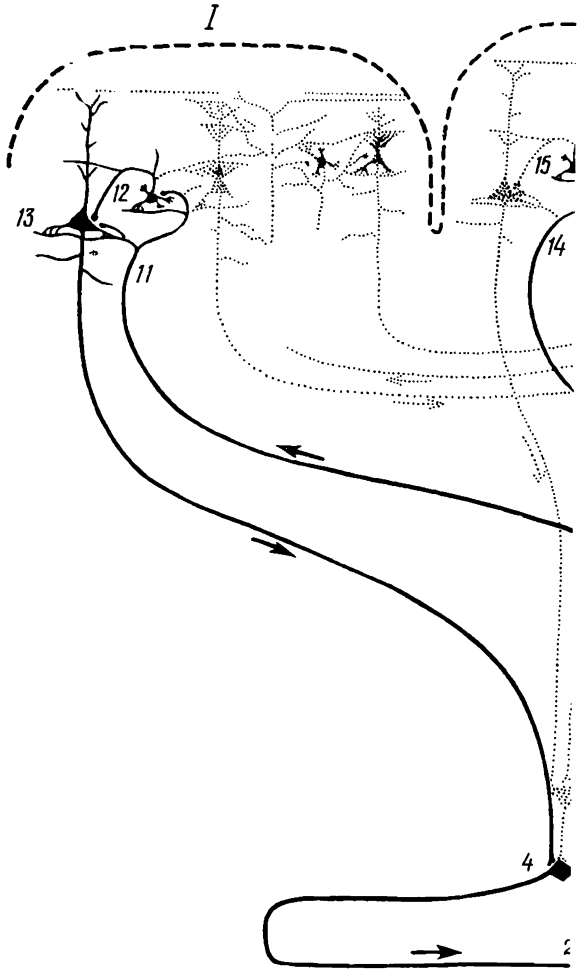
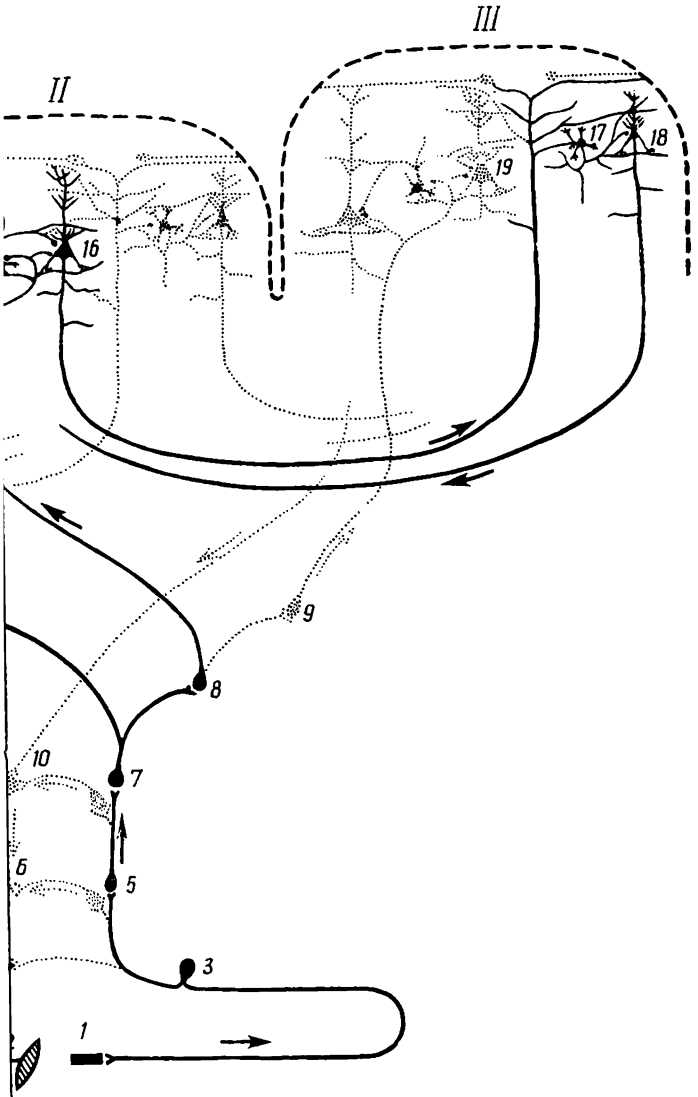


Plate VI. Diagrams of topographical relations in the CNS betw
(cortico-subcortical), and intracortical connections. The neurons n
of other systems (represented by dotted lines); *1*, receptor; *2*, eff
ching neurons of the axial part of the CNS (spinal cord and brain
tions (nuclei of the thalamus and geniculate bodies, subcortic
entering the cortex from switching stations in the subcortex; *1*
projection neuron (pyramid of layer *V*) giving rise to a cortico-m
sociation neuron of a higher levels of the cortex (pyramid of sub-
central field of the cortical zone of the analyser; the system of pr
—*2*); *II*, secondary (peripheral) field of the cortical zone of analy
out (*1—3—5—7—8—14—15—16—19*); *III*, field of the zone of
tions is depicted (*19—17—18*). The successive lengthening of the
dary (peripheral) and from them to the zones of overlapping (Po



een the complexes of neurons effecting association (intercortical), projection haking up each system are indicated by black lines on a background of those ector; *3*, peripheral sensory neuron; *4*, effector (motor) neuron; *5*, *6*, swit-stem); *7*, *8*, *9*, *10*, switching neurons of the supra-axial subcortical forma-al ganglia of the cerebral hemispheres); *11*, *14*, afferent projection fibres *12*, *15*, *17*, stellate neurons providing intracortical connections; *13*, cortical otor tract; *16*, cortical association neuron (pyramid of sub-layer III_3); *18*, as-layers III_2 and III_1); *19*, afferent association fibre entering the cortex; *1*, ojection connections of the cortex is singled out (*1—3—5—7—11—12—13—4* ser, the system of projection-association connections in the cortex is singled overlapping of the analysers; the cortex's own system of association connec-chains of switches is shown with the transition from central fields to secon-liakov, 1961).

direction, we understand those forms and components of behaviour that become fixed in evolution in the form of complex chains of innate adaptative reactions of the greatest significance for the life both of the organism and of the whole species. These vital reactions include all instinctive forms of behaviour, the programmes for which are fixed as the result of centuries of past experience and are passed down from generation to generation by inheritance. In man this type of reactions is involuntary to a high degree.

Auto-direction is very clearly expressed as the basis of behaviour in certain of the higher invertebrates (e.g. insects). In them an automatism of behaviour is observed so perfect, so 'polished' by the process of natural selection, as to create an impression of 'pseudo-thought'. Among vertebrates, fish, and then birds, have utilized a similar heritage of historically developed forms of automatism most effectively to adapt themselves to their environment.

The anatomical basis of auto-direction in vertebrates is, as already noted, the phylogenetically older cortical and subcortical formations of the end-brain (see Fig. 22), which include the formations of the palaeo- or semiseparatus, and lower levels of development of the separated cortex (the archicortex, or hippocampus, and the intermediate cortex, to use Filimonov's classification—1949), plus the sections of the subcortical ganglia of the hemispheres and the between-brain continuous with them (the amygdaloid bodies, the phylogenetically older nuclei of the thalamus, and the nuclei of the hypothalamic region). Among higher vertebrates (mammals) the cerebral substratum of auto-direction may also include, to a certain extent, some of the lower (in functional importance) formations of the neocortex. We have in mind its marginal zones (see Plate IV and Fig. 46)—the limbic and insular regions—plus the formations of what is known as the medio-basal cortex (certain sections of the frontal and temporal cortex on the medial and basal surfaces of the hemispheres); these sections of the brain, as has been shown in a number of recent experiments by Pribram (1961,1964) and others, have a direct bearing on the morphological and physiological mechanisms of vital reactions and emotional behaviour.

Instinctive forms of behaviour vary widely in composition in vertebrates of different levels of development; the morphological and physiological basis of auto-direction

correspondingly differs in the various animals. From the standpoint of unity of structure and function it is interesting to note that it is precisely in those vertebrates whose behaviour is determined by auto-direction that the end-brain consists of formations that are predominantly specialized for inherited fixation of species experience. In fish the still relatively weakly developed end-brain (see Fig. 6) consists of the oldest formations of the cortex semiseparatus; in birds, however, almost the whole mass of the cerebral hemispheres is formed by hypertrophied subcortical ganglia, while the cortical formations have undergone considerable reduction even in comparison with reptiles.

7. Direction Proper ('Free' or Voluntary and Automatized Direction)

In the broad field of direction in the proper sense of the word two sub-fields can be distinguished: (a) 'free' or voluntary direction (conscious in man), and (b) automatized direction (realized unconsciously in man).

By 'free' direction we mean the behaviour that is conditioned by the whole concatenation of changes in the environment, not only those occurring at the given moment but also those reflected in past experience. A precondition of such behaviour, which is mainly founded on complex systems of conditioned reflex associations, is the capacity of the organism to orient itself among those features of the surrounding medium that characterize its 'personal', individual life. The programmes of this behaviour are determined by innate reactions only in their most general tendencies. Correspondingly, the most essential distinction between 'free', voluntary direction and 'unfree', automatized direction, is that the first is elaborated individually on the basis of learning and the accumulation of living experience. Through voluntary direction the whole assembly both of 'natural' reflex coordinations inherited by the organism from its ancestors and the 'artificial' ones established by conditioning in the course of its life are brought into service in the basic task of adapting itself to its individual conditions of existence. Thus a given form of direction is really manifested in a programming of behaviour based on the joint activity of analysis and synthesis of stimulation and closing of conditioned reflexes.

It needs to be stressed that the concept of 'voluntary direction' embraces a variety of forms of behaviour ranging from the 'so-called voluntary' behaviour of animals (Pavlov) to specifically human conscious activity mediated by speech.

Sechenov called those movements voluntary that were directed to a definite perceived goal and were themselves objects of awareness. Pavlov included in the concept of voluntariness the higher analysis and synthesis of signalling occurring at the level of the cortex and providing information on each moment of the movement being performed. In the view of a number of Soviet psychologists—Leontiev (1959), Vygodsky (1960), Zaporozhets (1960) and others—man's voluntary acts are governed by an image of the end result and involve participation of the second signalling system. Beritov (1961) also considers voluntary all those behavioural reactions that are conditioned by the reproduction of models (images) of external objects in the cerebral cortex. Operations of a voluntary character with objects he calls 'instrumental actions'.

Thus the function of voluntary direction is realized as the end result of an analytical and synthetic processing of signals received from the sense organs and taking place in the higher cerebral ends of the analyser systems.

In Ashby's definition the function of direction can also be represented as the activity of a 'thinking system' that is in a state to make an appropriate choice on the basis of effectively processed information received. He includes man's ability to think rationally in the sphere of human direction. In human society one of the oldest and most important forms of directed activity, i.e. of direction in the sphere of relations with other people, is the process of education and learning by which the formation and development of psychic activity and the individual features of personality are moulded.

Berg (1963) characterizes direction as a process of translating a complex dynamic system from one state to another through action on its variables.

Trapeznikov (1963) distinguishes three basic groups of operations in the complex process of direction in both living organisms and in machines: study of the directed object; the working out of the strategy and tactics of direction; and their realization. The organism as a whole is looked

upon as a system of optimum control (in the ordinary, but not our, sense of the term).

Bernstein's conception is essential to an understanding of the role of direction in shaping active behaviour. In his view such behaviour is conditioned by the situation but not completely determined by it; the organism thus has a role in the resolution of definite operative tasks which are represented as models of the 'required future' 'coded' in the brain. The solution consists, in his view, in the two following basic factors: (a) prediction of the probability of the future situation from the information being currently received, i.e. extrapolation of changes in the situation at a certain interval of time ahead; and (b) the programming of the action that should lead to achievement of the goal of the action, i.e. which is an interpolation between the existing situation and that which is 'needed' by the individuum. The organism consequently does not simply react to the situation or to the stimulation of signal significance extracted from it; it is faced with a need to consider the dynamics of the changes in the situation and to make a prediction of the latter's probable course, and then to choose a line of behaviour. An evaluation of the future situation no more exact than with a certain degree of probability, and active choice of action that meets the situation and is not conditioned by its command signal—that, in Bernstein's view, is what essentially distinguishes the active behaviour of a living organism from a reactive machine of any degree of precision or complexity.

For our part we suggest that this mechanism of comparative evaluation of the present situation with the one desired, and the interpolation and choice of action, in a characteristic way distinguishes the behaviour of the higher animals most dependent on the function of direction proper from that of lower animals in which this function either does not yet exist or is weakly developed. It is also typical of the behaviour of lower animals, in contrast to higher ones, that it is not only conditioned by the existing situation but also determined by it to a considerable degree (or even completely) (see section 9 of this chapter). In other words the lower animal can make predictions about the probable future (and programme its behaviour accordingly) only to a very insignificant extent.

Automatized direction is built up from a series of conse-

cutively linked formulae of motor coordinations, 'artificially' established during life, in which inborn reflexes are utilized as 'raw material'.

To analyse the processes by which voluntary movements and acts become automatized, with their concomitant transformation into involuntary acts, it is necessary to go into the theory of coordination levels of the CNS (and the corresponding 'recoding' of series of impulses passing from one coordination level to another) worked out in detail by Bernstein (1947).

As Bernstein suggests, the fixing of a habit is not a simple learning of one motor act or another through repetition, but a process of constant improvement of a definite motor programme, i.e. active search for more and more adequate and optimal rational means, and variants of the solution of the task (in the form of trials, adjustment, and adaptive modulation, etc., in the pre-automatization period). In his definition the process of automatization is one of stage by stage switching of the 'background' components of a motor act at the levels of the appropriate corrections, which is effected by means of adequate sensory syntheses and programming devices.An example of the kind of corrective switching involved is the transfer of performed operations from the level of the spatial field to that of the body schema itself, when the mastered motor habit begins to be performed without active visual control. Various transfers of capacity for training ('drilling through habit') are possible, that is to say, the employment of automatized acts already established for other skills to build up new ones (e.g. riding a bicycle and speedskating). Bernstein also counts locomotion among the ready-made background components mastered at an earlier period of post-natal development and subsequently utilized to establish new skills and habits.

The more fully and surely a motor habit is mastered the richer is the fund of 'coordination resources' and the wider the round of variants and complications of tasks that preserve the achieved degree of automatized performance undisturbed. In that way a broad range of adaptive variability is ensured in all the components of established habits and operations.

By stabilization of a habit is understood the degree to which it is resistant to influences (or obstacles) tending to de-automatize it. The concluding stage of the process

of automatization is brought about by the harmonizing of the whole ensemble of background levels and by standardization of the motor composition of the habits involved. Standardization of habits is linked with reinforcement of the succession of fixation tensions in the appropriate synergistic muscles, which restrict the movement of that part of the body to a given direction; in this an essential role is played by the more flexible physiological mechanism through which it becomes possible to utilize the variety of reactive and inertial forces arising during performance of a movement in order to correct it.

Beritov qualifies the process of automatization as a chain of conditioned reflexes by means of which voluntary acts are reinforced through repetition many times in the same situation. Such automatized involuntary behaviour is suppressed as soon as its usual situation is changed; then the behaviour of the animal begins to be determined by active orientation to its surroundings, which finds expression in an active choice of actions directed by images of the corresponding objects.

Learned motor coordinations, which are initially formed under the influence of stimulation coming from voluntary direction, only secondarily (as already mentioned) take on an involuntary 'machine-like' character through exercise and training, and are performed (in man) without the constant active participation of consciousness. Processes of a similar kind also underlie the formation of a variety of skills (occupational, athletic, etc.). The more complex automatized acts built up from a series of motor coordinations include the behaviour of a hypnotized subject (see the next section). Another example of completely automatized forms of behaviour performed without conscious direction is a sleepwalker walking on the cornice of a building.

The category of automatized direction would also seem to embrace the very complex intracortical 'psychic coordinations' (based on the joint activity of appropriate groups of neurons) that form the material base of the intellectual operations performed in the cortex of the brain. We have in mind here the 'mental actions' (Halperin, 1957) that are initially performed, in the course of becoming established in a child, as real operations with objects ('materialized actions') with the constant involvement of consciousness. Subsequently

these operations are transformed from external into internal ones ('interiorized'), and 'rolled up', no longer requiring constant voluntary direction.

It follows from our conception of the process of automatization that there is a distinction in principle between automatized direction and the innate behavioural automatisms that characterize auto-direction and are predetermined on the whole by inborn biological tendencies belonging to the species as a whole.

On the physiological plane one must consequently differentiate strictly between automatic and automatized processes in animal organisms, although both types of phenomenon belong to the sphere of the organism's involuntary reflex activity. The first, unlike the second, do not require preliminary learning since the organism is born with ready-made formulae determining the sequence of appropriate reactions. All the auto-regulatory and auto-controlling apparatuses of the axial part of the CNS work to a greater or lesser degree on the principle of reflex automata, which also, as has been shown, underlies the functions of auto-direction.

Any conditioned-reflex reaction formed with the involvement of voluntary direction (new 'artificial' motor or secretory coordination) can also be looked upon (as regards the mechanism of its origin) as the expression of a special kind of 'automatism', with the proviso, however, that the automatization here affects components of the closure process that do not form part of the total experience of the species as a whole. On the contrary, the forms of behaviour arising as a result of fixation of species experience by inheritance (like the complex chains of instinctive reactions) are—together with the 'natural' reflex coordinations included in them—true automatisms.*

In the more highly developed vertebrates (mammals) the brain substratum of both voluntary and automatized direction is represented by the formations of the fully developed neocortex of the cerebral hemispheres (see Fig. 24)

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* In contrast to our terminology, which is based on a classification of the various components of the function of direction derived from evolutionary and biological premises, Bernstein also treats as automatisms those motor acts that are elaborated as a result of automatization of learned reactions.

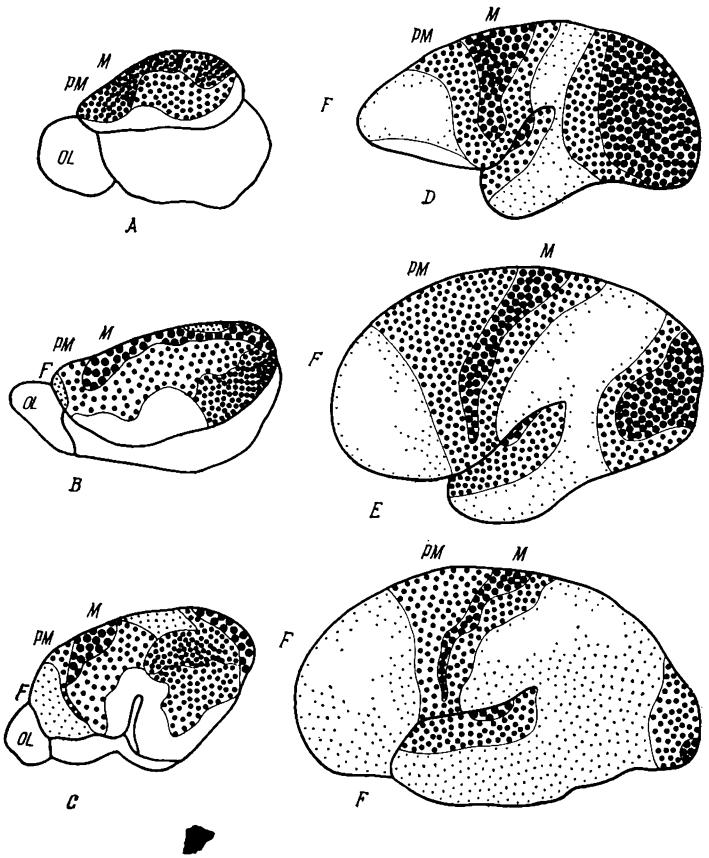


Fig. 24. Schematic maps of the progressive differentiation in the neocortex of a number of animals of cyto-architectonic regions and fields differing functionally in significance; *A*, hedgehog; *B*, rat; *C*, dog; *D*, monkey; *E*, anthropoid ape; *F*, man; *m*, motor cortex proper (large dots); *pm*, 'premotor' cortex (medium dots); *f*, frontal region proper (light dots); *ol*, olfactory lobe. The motor and premotor fields make up the motor zone of the cortex, while motor zone and the frontal region together make up the frontal lobe of the brain (Poliakov, 1960).

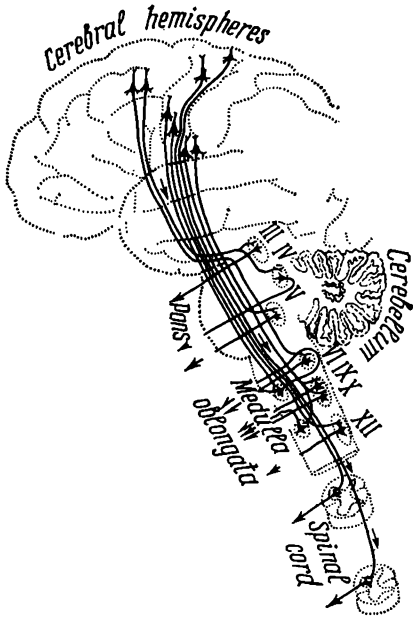
(which develop much later in phylogenesis and are more complexly differentiated along the lines of layered-screen type) together with their connections with the subcortical formations of the hemispheres and the between-brain (the upper subcortex), and with the lower-lying formations of the analyser-coordination and coordination mechanisms (lower subcortex) (see Figs. 25, 26).

In the fully developed neocortex the apparatus of direction is related, as we suggest, to the part of the brain most intensively developed in the evolution of mammals, i.e. to the frontal lobes.

In lower mammals this part of the brain is still quite weakly developed and is mainly taken up by the motor zone of the cortex (Fig. 24, *A* and *B*). In higher mammals—carnivores (Fig. 24, *C*) and primates (Fig. 24, *D*, *E*, *F*)—this zone is differentiated as the basic cortical mechanism for producing 'voluntary', finely differentiated separate movements (the motor cortex proper) and highly synthesized complex movements (the so-called pre-motor cortex). Both attain a high degree of specialization in the highest mammals, i.e. in primates, and especially in man. In the anthropoid apes, which already have well developed cerebral hemispheres resembling human ones in shape, the size of the frontal lobe considerably increased in connection with the development of its phylogenetically newer parts located around the frontal pole, and forming the frontal region proper of the hemisphere (see Fig. 24, *E* and *F*).

As the many years of clinical observation of Luria and his co-workers (1962, 1963) have established, the frontal lobe of the brain as a whole has a special role in the organization of the whole sphere of man's active, voluntary activity, from the simplest voluntary movements realized through the motor cortex proper to the most complicated phenomena of purposive activity effected by the frontal region and involving the second signalling system. This part of the brain is linked with the establishment and realization of plans of behaviour and the checking of the results of activity against intentions. It has also been demonstrated that a definite part of the motor zone of the cortex (the pre-motor cortex mentioned above—see Fig. 24, *pm*) plays an essential role in the processes of automatizing voluntary movements.

Fig. 25. The pyramidal tract, which serves to transmit direction impulses from the cerebral cortex to the reflex centres of the brain-stem and spinal cord, that form part of the coordination mechanism. Roman numerals indicate the motor nuclei of the corresponding cranial nerves. To simplify the diagram the switching neurons of the reticular formation have not been represented (modified from Bekhterev).



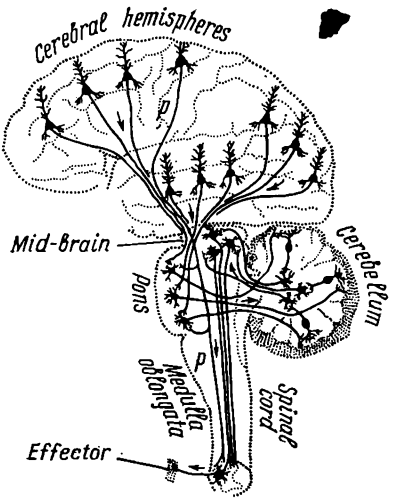


Fig. 26. Scheme of the extra-pyramidal tracts that serve to transmit direction impulses from various regions of the cortex to the analyser-coordination mechanism (cerebellum). The chain of successive switchings of impulses from the cerebral cortex to the cerebellar cortex and from the latter to effector neurons is represented; *p*, pyramidal tract (after Ramon y Cajal, with modifications).

The morphological basis of the higher organizers of behaviour is provided by the fields of the frontal region proper with their highly complicated two-way connections with the cortical and subcortical representations of all the analyser systems, the representations in the brain of vital reactions, and the mechanisms of reflex coordinations

located in the lower levels of the CNS. In man these fields occupy around a quarter of the whole neocortex.

Over the past hundred years thousands of pages have been devoted to description of the functions and structure of the frontal lobe of the brain. In our view the most satisfactory definition of the functional role of this 'powerful' part of the brain is direction; and we regard it as that division of the whole central nervous organization which has been specialized in the course of evolution for realizing the most complex forms of the direction function (both 'free' and automatized) in all its varied manifestations.

In the various kinds of lesion of the frontal regions the foreground of the clinical (psychopathological) picture is occupied by disturbances of the various forms of voluntary acts. It should be noted that a definite role in the rise of these disturbances is played by defects of the afferent syntheses already developed before the beginning of activity involving major participation of the frontal formations (Luria). Essential to this is the breakdown of the associative connections by means of which the functional correlations of the higher forms of gnosis, praxis, and speech are realized. Disturbances of this kind are conditioned by pathological alterations in the most complex psychic processes of perception, memory, thought, and action.

One of the most demonstrative manifestations of disruption of the function of voluntary direction in brain lesions that affect the frontal regions of the cortex and their connections to a considerable degree is the dissociation of the intellectual, emotional, and volitional spheres in schizophrenia. The essence of that peculiar disease is, it seems to us, that the intellectual apparatus itself remains more or less intact but the patient loses the possibility of making adequate use of it.

The impulses of voluntary and automatized direction are produced, as already explained, by way of the numerous links connecting the higher cortical apparatus of direction with all formations of the upper and lower subcortex, i.e. with the coordination and analyser-coordination mechanisms and the morphological base of auto-direction. By means of these connections this cortical apparatus is able to influence the body's effector instruments in a more or less selective, differentiated way, depending on the stage of development of the organism's effector sphere. In the

evolution of mammals a special pathway is developed for conducting the impulses of voluntary movements (which attains particularly marked development in primates), i.e. what is known as the pyramidal tract uniting the motor and other regions of the cortex with the effector (motor) nuclei of the brain and spinal cord (Fig. 25). This system of fibres runs both to effector neurons directly innervating the skeletal musculature and to the switching neurons of the reticular formation of the brain and spinal cord i.e. to elements of the coordination mechanism (see Fig. 11*B*). It has been established by experimental morphology that the apparatus of direct cortical influence on effector neurons becomes more and more pronounced as mammals become more highly organized; this finds anatomical expression in an increased number of endings of fibres of the pyramidal tract at those neurons, apart from endings at internuncial neurons of reticular form.

The cortex of the brain exercises a constant tonicizing or depressive effect on the state and activity of all lower reflex centres. In that the motor zone of the cortex has a special role, since it is linked with them in the most direct way. It has been established in particular that the corticomotor (pyramidal) tract is a source of constant bio-electrical activity by means of which reflex centres are maintained in a state of latent readiness to react rapidly to stimulation. By means of additional influences coming from the cerebral cortex to the centres of the vegetative nervous system definite states are ensured in the reacting organs (metabolism, blood supply, trophic processes) that favour the fullest realization of the reflex potential of the organism.

In addition to the pyramidal tract, which links the higher cortical ends of the analyser systems in the most direct way with the corresponding sections of the coordination mechanism, so-called extra-pyramidal tracts are considerably developed in the CNS, especially of the higher mammals. They run from the cerebral cortex to the axial part of the CNS and are mainly directed to the various formations of the analyser-coordination mechanism. In primates leading an arboreal life, or walking erect, the most important of these pathways are the connections with the cerebellum, which take their beginning in various regions of the neocortex (Fig. 26). The fibres of the pyramidal tract, by-passing to analyser-coordination formations, also give off

many collaterals to corresponding groups of neurons at various levels of the CNS.

The extra-pyramidal connections of the cortex with the analyser-coordination formations (in particular with the cerebellum) play a most essential role in the processes of automatizing voluntary motor acts. It can be assumed that the mechanisms of regulation and control are no less important for automatization of voluntary movements and actions (in the sphere of animal life); on the anatomical plane that means that realization of the formulae for translating (recording in Bernstein's terminology) effector activity from voluntary into involuntary automatized acts, which are elaborated in the cortical ends of analyser systems, depends essentially upon those collateral connections by means of which the analyser systems influence the mechanisms of reflex coordination along the axial part of the CNS.

Impulses of voluntary direction 'triggering' a chain reaction of automatization pass to various components of the auto-regulatory and auto-controlling devices, with different degrees of 'penetrability'. The automatically operating reflex coordinations to which auto-regulations of the body's internal vital activities above all belongs are not subject (or only slightly) to voluntary influences, unlike consciously directed reflex processes. Experiments carried out in Asratian's laboratory have established that the participation of the cortex in compensatory processes linked with disturbed functioning of internal organs is much less pronounced than in respect of outwardly directed reflex activities.

We would suggest that the forms of direction reviewed above can be reproduced by means of an experimental technical model. The designer of such a model must, consequently, create a block of automatic direction with built-in fixed programmes of behaviour, then a block of direction proper providing means for the machine to learn with subsequent automatization of the learned activity.

8. Psychophysiological Aspects of the Problem of Direction

The problem of studying the real interrelations between the various forms of direction in animal organisms is a most promising one, not only on the purely physiological

plane but also on psychophysiological one. As a matter of fact, the round of questions touched upon could also include those branches of psychology that concern themselves with the organization of planned, purposive activity, anticipation of the probability of certain events occurring*, the connections between the voluntary and the involuntary, and the conscious and the unconscious in active psychic acts, and the internal interactions between the volitional, intellectual, and emotional spheres.

The relations between the conscious (voluntary) and unconscious (involuntary) would seem to be of most vital significance for understanding all aspects of the complex problem of direction. Here we take as our starting point the observations and experiments of Gershuni (1949) and others who have studied subsensory responses to sub-liminal stimuli and demonstrated the existence of processes of cerebral activity taking place latently below the threshold of consciousness and anticipating the occurrence of psychic acts reflected in consciousness, namely, feelings, perceptions, logical deductions, and purposive acts. Processes, of which we are unaware, i.e. those that have already, in our conception, passed the stage of initial automatization ('psychic automatisms' in Janet's definition) play the role of a kind of ground work evolved in the ontogenesis of the individuum on which a whole chain of causal connections develop between the successive stages of whatever voluntary act is being performed.

Closely related to the problem of the relations between the conscious and unconscious in the function of direction is Bernstein's theory of coordination levels already mentioned. In any complex voluntary act only that which is related to the leading level of the action performed is done consciously. All other subsidiary levels ('background') are involved as unconscious components, i.e. they remain as it were in the shadows beyond the 'spotlight' of consciousness. Only that which has to be performed is fixed in consciousness, and not how the appropriate activity (practical or intellectual) is to be performed. We are aware not of the separate components of the actions performed, but only of their logical sequence.

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* We have in mind the special extrapolational reflexes studied by Krushinsky (1959, 1960).

To that it can be added that no voluntary action of man is at the same level of awareness at all stages of its gestation and performance. We are most aware, as a rule, of the immediate stimulus to activity and of its completion as a real expression of achievement (or non-achievement) of the goal to which the action was directed. The problem of awareness of the different stages of a voluntary action is obviously very complex both as regards methodology and as regards methods and is far from being resolved. The various acts voluntarily performed probably vary widely in the number of components that can be simultaneously represented in consciousness.

The definition given above of 'automatized direction' far from exhausts the possibilities of effecting direction unconsciously. In particular it would seem, for example, that hypnotic suggestion can be considered a peculiar psychophysiological state in which the work of the higher apparatus of direction is transferred from the level of consciousness to the subconscious while fully preserving the formal structure underlying performance of the operation. It is known, of course, that hypnotized subjects are able to retain quite complicated instructions in their memories for quite long period, and although these remain completely unconscious they can nevertheless be performed with great accuracy. Means are consequently conceivable in which the whole reaction directed from the cerebral cortex takes place from beginning to end without clear awareness of the signal significance of the stimuli that produced it or of the meaning of its effect.

Another example of the actual complexity of the function of human direction is the dual psychophysiological state of the actor in connection with his special distribution of consciousness and attention during his stage actions. The actor playing his role on the stage must (in Stanislavsky's system) acquire the faculty (by way of long preliminary training) of voluntarily evoking experiences, moods, and emotions of one kind or another in himself while remaining, at the same time, unmoved by them, in contrast to natural behaviour in ordinary life. One great actor formulated this position as training the body to perform any command dictated by thought and will; the actor has to be master both of himself and of his own forces.

Stanislavsky himself often used to refer to this in the words of the famous Italian tragedian Salvini: 'When I act I live a double life; I laugh and weep and at the same time I am analysing my tears and my laughter so that they can even more strongly affect the hearts of those I want to move'.

The series of experiments described below can be taken as a good illustration of the problem of the mechanism of voluntary evocation of involuntary reactions in animals.

A conditioned reflex to the sound of a metronome was established in a dog; at its sound the animal was required to jump onto a table where there was food. On getting down from the table the dog usually shook itself. When the metronome was sounded at that moment with subsequent reinforcing with food, a functional association was established between the involuntary reaction of shaking itself and the sound signalling food. This led to the dog shaking itself more often (up to twelve times in a single experiment). After a year the animal could actively reproduce this involuntary movement with such ease and exactness that it gave the impression of a 'voluntary' motor act.

It can be assumed that there are three levels of interrelations between the conscious and unconscious components in the integral function of direction, each of which has its own characteristic degree of subordination of the unconscious ones to the conscious.

The lowest level, formed in the earliest stage of the evolution, is represented (in more complexly organized creatures) by the influences of an involuntary character that the higher sections of the brain undoubtedly exert on the whole vegetative sphere of the organism. We have in mind the influence of the cerebral cortex on the most intimate processes of the internal life of the body. States of affect, suggestion, and hypnosis, for example, are accompanied with alterations in the level of blood sugar (Platonov, 1962).

The following experiment can illustrate this kind of influence. In a dog with an undamaged CNS the composition of the gastric juice secreted varies in accordance with the character of the food given to it. But after removal of the cerebral cortex differential secretion ceases to occur and the animal secretes the same gastric juice for all foods.

It is quite evident that the deeply latent form of direc-

tion noted above takes place from beginning to end as a completely unconscious process not directly dependent upon the will. The role of the voluntary component is approximately nil; in other words, liberation of the involuntary component from the influence of the voluntary one finds its maximum degree of expression here.

The material substratum of these 'hidden' cortical influences, which attain great force in certain psychic states, probably coincides with the apparatus linking the appropriate formations of the neocortex with the phylogenetically older ones in the cortex and subcortex, the hypothalamic region, and the reticular formation.

The middle level, which can also be characterized as a transitional one between the lower and higher ones, is represented by those forms of direction in which the involuntary and unconscious are only partially subordinated to the voluntary and conscious. In the emotional sphere, we have such a correlation of the two kinds of component, and their different variants, particularly in the influences exerted by the cortex on feelings and mood, and on the degree of 'tension' in experience. The various emotional phenomena usually arise involuntarily in the depths of the subconscious, but to some extent are subject to voluntary influences, i.e. may be suppressed or inhibited or, on the contrary, strengthened.

Finally, the highest level which is formed last in evolution and only appears fully in the phase of the origin and development of human kind, is mainly related to voluntarily performed movements and actions. At this stage of complication of the material mechanism of consciousness, the involuntary components are subordinated to the maximum to the voluntary. This category of involuntary and unconscious components of voluntary acts can be held, on the whole, to include, in the broadest sense, the concept of automatized direction formulated above, i.e. in the sense of the automatization not only of actions but also of logical processes.

The motor acts elaborated are, as we have already said, excluded from the sphere of moment by moment awareness and transferred to the level of automatized processes.

The highest level of the direction function also includes, to all intents and purposes, the various intellectual operations the structure and realization of which can be

assumed to include both voluntary and involuntary (automatized) components. Obviously, not only actions can be automatized and carried out below the threshold of consciousness, but also, within certain limits, intellectual operations (acts of perception, comprehension, and memory). In particular the famous 'unconscious deductions' of which Helmholtz wrote can be included in this type of phenomenon.

In certain situations presenting higher demands on the speed of processes of perception and comprehension these psychophysiological mechanisms acquire special significance. The job of a pilot controlling a jet aircraft requires superfast, lightning orientation, grasp of the situation, and taking of decisions. As astronaut Gherman Titov has put it, the modern fighter pilot has to build up his own special 'automatism' in which thinking merges as it were with action, and in relation to which it 'is difficult to establish which comes first, action or thought'.

It can be supposed that one of the main directions in the further progress of human nature and central nervous organization will be that of still greater functional improvement of the cerebral apparatus of direction. This process will probably be a natural precondition for man's mastery not only of the universe but of himself, i.e. of the reflex potentials accumulated in his material organization, and in the direction of ever greater subordination to voluntary control of those aspects of reflex activity that are not yet subordinated to it, or only weakly so. It is not out of place to recall a remark of Pavlov's here. With his customary ability to get to the heart of things Pavlov wrote that understanding of the nature of instincts would 'enable us to understand ourselves and the development of our capacity for personal self-control.'

9. The Relation of the Functions of Auto/regulation, Auto/control, and Auto/direction from the Standpoint of Evolution

In the lowest multicellular animal organisms with a primitive neuronal organization (Coelenterata and Echinodermata) ability to control their own behaviour in any real sense is still, apparently, very weakly developed. These organisms are a kind of living automaton (highly perfected in

a 'technical' sense), capable of performing only primitive forms of adaptation to changes in the situation around them. The elementary character of their reactions is conditioned by the fact that the latter are a direct response to the stimuli acting at a given moment. These creatures are not in a position to take into account the changes in the situation that may ensue as a consequence of their reactions. In other words, they still do not possess centralized behaviour. Their existence proceeds, as it were, in momentary segments of space-time.

The uncentralized netlike nervous system of coelenterates still shows no signs of cephalization, i.e. it has no head sector; it can be described as weakly auto/controlled and even more weakly auto/directed. Fundamentally this primitive form of neuronal organization, which already has the property of bringing about a coordinated reaction to adequate stimulation, works on the principle of an autoregulatory apparatus. Uexküll (1928) figuratively compared the aggregate of an echinoderm's (sea-urchin's or starfish's) reactions to 'a republic of reflexes'. It can be supposed that the reflex possibilities of these animals have scarcely gone beyond the limits of an elementary coordination mechanism.

Despite their still weakly developed 'spontaneous' activity and lack of capacity to perform purposeful activity, the lowest multicellular animals do display a certain variety of distinct, though primitive, reflex coordinations linked with their ecological conditions.

An indispensable anatomical and physiological prerequisite of the development of functions of auto/control and auto/direction is the differentiation within the neuronal organization of a special central sector in which signals received from the various sensory organs are combined and more complicated synthetic formulae of response are worked out. This sector is the brain, which first begins to take shape at the stage of the band-like nervous system in the lower worms, in which a primitive degree of centralization of neurons is observed, and of which can be said that it leads to the development of rudimentary analysers.

A brain 'control panel' (in the broadest sense of 'control' and 'direction') begins to be more distinctly defined in invertebrates that have left the water for the land and

already possess a more complexly organized ganglial nervous system (segmented worms).

The higher invertebrates (crustaceans, insects, cephalopods) already have rudimentary analysers represented by definite formations in their brains. And we can say that these animals have quite clearly delineated (though still primitive by comparison with vertebrates) functions of auto-control and auto-direction, with certain, still weakly expressed elements of direction. These functions are related to various sectors of their cerebral ganglia. The subglottal ganglia (see Fig. 2) (which we regard as the representatives of an elementary analyser-coordination mechanism) are predominantly related to auto-control; the supraglottal ganglia, with which are linked the reception and processing of distance recepts (smell and vision) and the integration of external perceptions with the internal states of the organism, perform the function of auto-direction.

A heightening of the capacity of the brain to influence the various reflex coordinations of the trunk ganglia directionally (by stimulation or inhibition) can be observed in the evolution of invertebrates. But the real 'organizational' premises for rapid progress in the development of functions of 'free direction' appear only in vertebrates. And only in those members of the animal kingdom that already have a much more completely centralized nervous system (by comparison with invertebrates) in the form of a neural tube with much more advanced cephalization do we find direction more or less developed. In the side shoots of this branch of the evolutionary tree (fish and birds) adaptation to the environment takes the line predominantly of auto-direction.

To sum up, it can be said that the greater complicating of the general plan of neuronal organization during phylogenesis is built up on the principle of triple subordination, i.e. on the basis of interaction of the functions of auto/regulation, auto/control, and auto/direction.

Several stages can be distinguished in the evolution of the animal population of our planet, which reflect the various levels of organization of behaviour.

At lowest level of development these functions are all still fused in one general complex, in which, however, the role of 'leader' is taken by the function of auto-regula-

tion, which is the first to be crystallized out in the course of evolution.

In the lower multicellular animals (coelenterates and echinoderms) this function dominates in their orienting, feeding, defensive, and adaptative reactions, and in the closing of conditioned-reflex connections. The principle of autoregulation, which has its anatomical and physiological basis in the coordination mechanism, is the decisive factor at these stages on which the establishment of reflex adaptations depends.

At later stages of evolution the function of auto-regulation (in the highest invertebrates and in all vertebrates) is concentrated in the lower, axial part of the centralized nervous system. The reflex adaptations performed by way of the coordination mechanism can be regarded as auto-regulating components of a closure process and also of orienting, adaptative, and other vitally important reactions. It should be noted, in particular, that the phenomena of summation effect and dominance connected with the coordination mechanism also appear as components of this kind; and in our conception, elements of the formation of reflex coordinations and of the closure of conditioned reflexes are fused together in them.

In the vertebrates lowest in development (Cyclostomata), the main role in reflex adaptations would seem still to be taken by the coordination mechanism, since the analyser-coordination formations and the supra-axial part of the CNS are fairly weakly developed in them. Correspondingly, the functions of auto-control and auto/direction are still at a very primitive level.

With the development of analysers, which constitute the material substratum of the higher functional potentials of the animal organism (by comparison with auto-regulation), the function of auto-control begins to develop intensively. This function would seem to reach its peak in the lower vertebrates (fish), which possess complexly differentiated analyser-coordination formations in the axial part of the CNS with a still fairly weak development of the supra-axial part (see Fig. 6). At that stage we can, consequently, already speak of auto-controlled components in the closure of a conditioned reflex and in orienting, adaptative, and other reflexes (i.e. of components involving the lower cerebral parts of the analysers). It can be considered that

those animals have already finally mastered the space around them. The components of the closure function performed at the axial levels of the CNS have been distinguished in a number of experiments (Karamian, 1956) in which the essential role of the cerebellum in the establishment of conditioned reflexes in lower vertebrates has been demonstrated.

The dominance of direction (with its auxiliary attributes of regulation and control) appearing later in evolution coincides with further progressive development and complication of the analysers. In mammals the most essential transformations of the CNS are linked with the structural and functional differentiation of the analyser systems, especially of their higher (supra-axial) cerebral ends. The higher brain mechanisms of direction proper reach their peak in primates.

At that stage of phylogenesis we can, consequently, speak of the ever growing role of direction, control, and regulation in the reflex coordinations of the axial part of the CNS. (In the side branches of the evolutionary tree represented by fish and birds auto-direction occupies the foreground.) The most highly organized components of orientation in, and adaptation to, the external world, which are manifested in the active mobile tuning exercised by the analyser systems on the perception of stimuli (and which underlies the physiological mechanism of attention and apperception), are formed with involvement of these functions. Correspondingly the activity of the cortical part of the closure process becomes more finely and complexly differentiated; and as a result the possibilities of individual reflex mastery by the organism are vastly extended not only in its past and present, but also in its future.

CHAPTER III

THE NEURONAL NETWORK

1. The Origin and Complication of the Neuronal Network

The most complex things are basically simple. But the researcher runs up against considerable difficulties in his efforts to grasp the elementary principles underlying even the most complicated phenomena. To overcome these difficulties he has, above all, to have a general idea, hypothesis, or theory that can put him in a position to explain the facts observed by him in a satisfactory way, and to mount experiments to test it.

In the science of the brain, as in other fields of natural science, the comparative, historical, evolutionary method of analysing and synthesizing the factual material accumulated is of immense value. Comparative study of the topographical interconnections (architectonics) and structure of neurons, and the character of their junctions in the peripheral, subcortical, and cortical sections of the analysers, together with the links (conducting pathways) between these sections, at various stages of the evolution of vertebrates enables us to trace certain morphological laws governing the complexity of the structures as a whole.

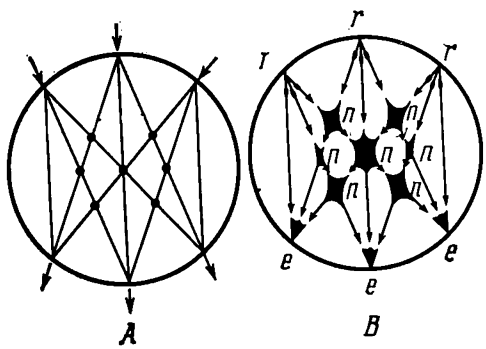
In our understanding of the origin and subsequent development, complication, and perfection of the structure of the brain as the material basis of the functional relations within the organism and between it and the external world, we are guided by the two following basic premises.

We consider that the biologically conditioned principle of universal linking-up of all the organism's elements (receptors) perceiving stimulation with all those (effectors)

effecting the responses to that stimulation is the very foundation of neuronal organization. Any receptor, or combination of receptors, can be linked with any effector, or combination of effectors. Anatomically this principle takes the form of a scheme of universal intersections ('grid' or 'lattice') of nervous pathways uniting the different receptor points of the body (or groups of them) with effectors (Fig. 27*A*). As will be shown in Chapter IV a scheme similar in principle underlies the geometrical construction of the links of switches and the conductors in the analysers linking them (especially in the analyser systems).

The capacity of the animal organism to adapt itself within wide limits and with great flexibility to a constantly changing environment and its potential readiness to react to every possible combination of external and internal stimulation finds real expression in the universal functional linking-up of receptors and effectors thus materialized in the brain matter.

Our second premise follows directly from the first, and is that the structural differentiation of all elements of reflex activity takes place at the same time. This premise includes the corollary that neurons, as the apparatus of links between receptors and effectors, are formed not ac-



F i g. 2 7. *A*, scheme of the lattice of paths distributing nervous impulses from receptor points of the body (three top arrows) to effector points (three bottom arrows); *B*, scheme of an elementary network of neurons, illustrating the rise of neurons at the intersections of the lines uniting receptors and effectors. Arrows indicate the direction in which impulses are switched; *r*, receptors; *e*, effectors; *n*, neurons

cidentally but in a completely law-governed manner at the nodes of the intersecting streams of impulses running from the receptor to the effector points of the body.

As can be seen in the diagram (Fig. 27*B*) neurons arise and become structurally reinforced precisely at the points of interaction of nerve impulses differing in both origin and destination. Thus the neuron from its very origin in the evolution of animal organisms appears to us as an apparatus of convergence and divergence of impulses which are switched in it. It can be taken that all neurons in actually functioning nervous systems (possibly with very rare exceptions) are interconnected and work on that principle. We would recall that the convergence of nervous impulses of various kinds on separate neurons, with their subsequent divergence, has been convincingly demonstrated in the various formations of the central nervous system (the cortex; and such subcortical formations as the thalamus, the subcortical ganglia of the cerebral hemispheres, and the amygdaloid bodies); and the reticular formation of the brain-stem. Particularly well expressed is the convergence of heterogeneous afferent impulses on the effector (motor) neurons, which Sherrington likened to a funnel. The synthesis of the many streams of impulses coming from receptors and various levels of the CNS taking place in a motoneuron has been figuratively compared by Bernstein to several performers playing with one bow on the same cello.

In the course of the progressive centralization of the nervous system, which is accompanied with an ever greater predominance of the mass of the brain over the spinal cord (cephalization), essential transformation of the network takes place in connection with the growing complexity of the interactions between neurons, both as regards the structure of the different neurons and as regards the whole system of interneuronal connections. These alterations (see Fig. 1) are expressed in an intensification of the terminal branchings of the peripheral afferent nerve fibres carrying impulses from the receptors and the protoplasmic processes or dendrites of the nerve cells articulated with them. At the same time the number of branches (collaterals) running from the nerve fibres, or axons of nerve cells located in the centralized nervous system itself, grows. As a result of this perfecting of neuronal organization ever closer

and more differentiated contacts are established between the different neurons jointly involved in the performance of definite reflex acts, and feedback circuits are closed with onward transmission of impulses along the reflex arcs. In that way the anatomical, physiological mechanism takes shape for lengthy retention in the nerve centres of traces of the excitations reaching them and for reproduction of the reactions elaborated. These features attain their highest degree of complexity, in comparison with the rest of the CNS, in the analysers, and especially in their cortical sections (see Chapter IV, section 2).

2. Progressive Differentiation of Neurons

In the lowest vertebrates the CNS is still fairly weakly differentiated (see Fig. 28*A*). The neurons receiving impulses from the periphery, distributing them within the CNS, and sending them back to the periphery, are still not distinctly distinguished from one another functionally. These elements can be characterized according to their structural features as having a transitional structure between that of effector and reticular neurons, still combining the properties of both. In subsequent stages of evolution structural specialization takes place in the composition of this primitive coordination mechanism, with a spatial separation of neurons with different functional purposes. The process takes place in the following three main directions (Fig. 28*B*).

On the one hand an executive part of the coordination mechanism is differentiated, represented by groups of effector (motor) neurons (Fig. 28*B*, *3*) directly innervating the motor and secretory organs of the body. On the other hand groups of central internuncial neurons are differentiated adapted to coordinating the interaction of the effector neurons making up the local segmental reflex apparatuses located along the axis of the CNS.

As already mentioned in Chapter I (see section 3), those neurons (Fig. 28*B*, 4) that make up the suprasegmental part of the coordination mechanism in their aggregate form the reticular formation of the spinal cord and brain-stem. The reticular neurons are included in local reflex arcs as supplementary intermediate links switching centripetal afferent impulses reaching the CNS from the receptors in-

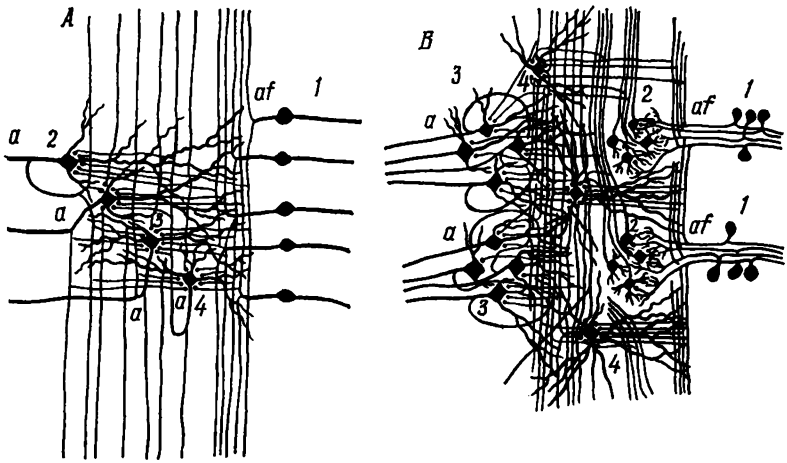
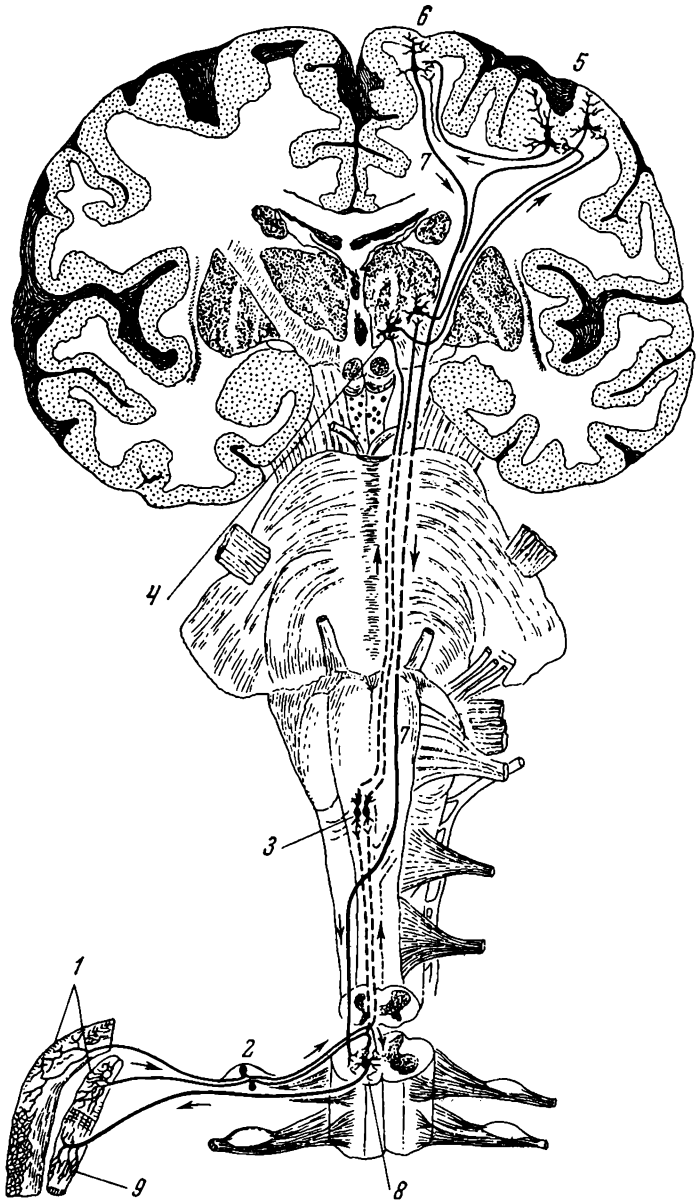


Fig. 28. *A*, neuronal structure of the central nervous system of lower vertebrates; *1*, peripheral sensory neurons; *2*, *3*, *4*, central neurons of a mixed type from which effector (motor) and reticular neurons are subsequently differentiated (see *B*); *B*, neuronal structure of the central nervous system of higher vertebrates: *2*, nodes of neuronal switches on the pathway of analysers; *3*, effector (motor) neurons; *4*, reticular neurons; *af*, peripheral afferent fibres; *a*, axons of neurons (after Poliakov, 1959)

volved and then distributed to the various motor nerve centres. These elements, together with the recurrent collaterals running from the fibres (axons) of the effector nerve cells, play a very important role in closing the feedback circuits (see Fig. 43*C* and *D*) in the reflex arcs of the spinal cord and brain-stem that is essential to coordinated performance of the various reflexes.

The development of analysers represents, as we know, a further stage in the progress of organization of the CNS, together with the ever more detailed differentiation of the groups of effector and reticular neurons that make up the local coordination reflex instruments. The systems of analysers take shape as an apparatus conducting and switching the most concentrated streams of centripetal nervous impulses.

The main mass of the elements composing the switching nodes united in the single through system of an analyser consists of efferent neurons (Fig. 29), transmitting impul-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ses to the next switching link in the chain. The axons of these nerve cells terminate at the switching station where they arrive as afferent fibres.

At all switching levels the efferent neurons of the analysers (Fig. 30*C*) are characteristically distinguished from the motor and reticular neurons (Fig. 30*A* and *B*; see also Fig. 18) making up the coordination mechanism by the much greater arborization of the dendrite tufts arising from the bodies of the nerve cells. The terminations of the afferent fibres, articulating with the dendrites of efferent neurons and having the typical shape of a bunch or cluster, are also characterized by considerable arborization. Another feature of the switching apparatus in the analysers deserving attention is the considerable development of side and recurrent collaterals from the axons of the efferent neurons, from which the main tracts for conducting centripetal excitation are built.

These features of the structure of the switching nodes in the analysers are conditioned, it would seem, by the high degree of concentration of the switched impulses and the complexity of their treatment in the course of transmission from one group of efferent neurons to another.

In favour of this view of the construction of the elements of analysers and their interconnections can be cited the results of Durinian's experiments (1963). By means of electrophysiological techniques (using registration of so-called 'evoked' potentials) certain essential functional and topographical relations have been distinguished between the groups of elements conducting and switching impulses that make up the analysers. In the conducting pathways and switching centres along the analyser system sections can be distinguished in which the nerve fibres and nerve

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Fig. 29. The systems of the cutaneous and kinaesthetic analysers (switching impulses received from the organs of motion). Efferent neurons with long axons are located as follows; *1*, endings of sensory nerve fibres in the skin and organs of movement (muscles); *2*, peripheral sensory neurons of a spinal ganglion; *3*, switching nuclei in the medulla oblongata; *4*, switching (relay) nuclei in the thalamus; *5*, the cutaneous and kinaesthetic (general sensory) zone of the cortex; *6*, motor zone of the cortex; *7*, pathway from the motor cortex to the motor centres of the brain and spinal cord (pyramidal tract); *8*, effector (motor) neuron of the spinal cord; *9*, motor nerve endings in the skeletal muscles (Poliakov, 1956)

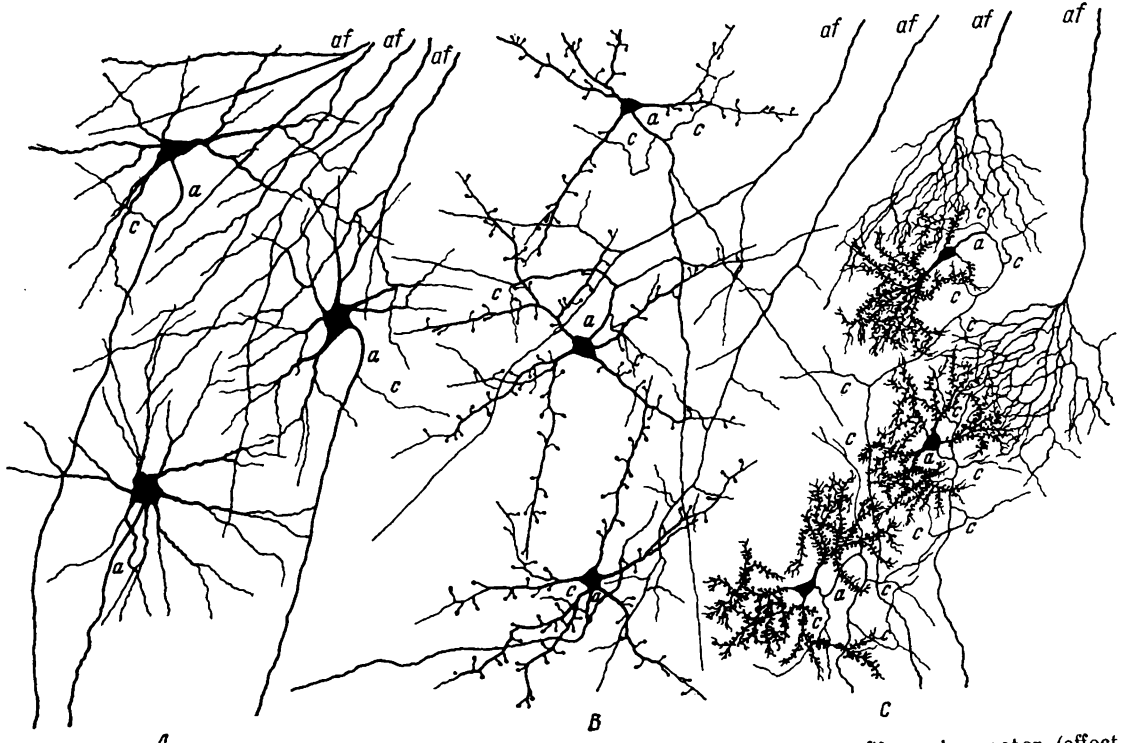


Fig. 30. Characteristic features of the structure of neurons and afferent fibres in motor (effector) nuclei (*A*), nuclei of the reticular formation (*B*), and switching nuclei of the analysers (*C*); *af*, afferent fibres; *a*, axons of nerve cells; *c*, initial (side and recurrent) collaterals of axons. Attention is drawn to the clusters of dendrite branchings in the switching stations of the analysers.

cells lie particularly close to one another. And it is precisely in these bundles and collections of cells that the most characteristically expressed bioelectric potentials are registered (the so-called foci of maximum bioelectric activity) when corresponding parts of the receptive surface or nerves are stimulated.

Because of the high concentration of nerve elements in foci of maximum activity conditions are created there favouring synchronous discharge of many elements. The electrophysiological expression of this process is the minimum latency period and maximum amplitude of deflection of the evoked potential. In those sectors of the CNS in which the distribution of neuronal switches is less dense, and they are more dispersed in relation to one another (for example, in the reticular formation of the brain-stem and in the so-called non-specific nuclei of the thalamus that form its continuation), foci of maximum activity are not found.

3. Internuncial Neurons and Their Role in Reflex Activity

Internuncial (intermediate, or intercalary) neurons form part of the chains of direct transmission of impulses along segmental reflex arcs and analysers as supplementary, superimposed elements. In the local reflex apparatuses of the spinal cord and brain-stem these elements are the reticular neurons mentioned above (see Fig. 3, *rf*; Fig. 7, *rf*; Fig. 10, *rn*; Fig. 15, *rf*); the main thing distinguishing them from effector neurons is that they have no direct exit to the periphery, their processes being confined to the corresponding part of the CNS, whereas motor neurons are always located in the offshoots of the CNS and send axons to the periphery, to the appropriate muscles or glands.

From the research of recent years it can be concluded as established that even the most elementary reflexes effected by way of a so-called simple two-neuron reflex arcs are only performed orderly when they involve internuncial neurons (which are represented in the axial part of the CNS, as has been shown, by reticular elements—see Fig. 11*B*, *3*). How much more significant then in the processes of coordinated interaction and transfer of impulses in the analyser-coordination mechanism and analyser systems, it would seem, must be the elements that we include in the general group of internuncial neurons. The existence of a

similar kind of element at sites where impulses are switched along the course of analysers has been demonstrated both by morphological studies and by electrophysiological research (Eccles, 1959; Kostyuk, 1962). Neurons have been found in the relay nuclei of kinaesthetic and tactile analysers located in the medulla oblongata, and higher in the cerebral cortex and other formations, that generate discharges of frequencies upwards of 1000 times a second in response to a single stimulus. As we have recalled (see Chapter I, section 3), high-frequency rhythmic discharges to a single stimulus are characteristic precisely of the reaction of internuncial neurons to stimulation.

Among the internuncial neurons in the analysers we distinguish elements of two kinds. We would draw attention, first of all, to the circumstance that typical, rarely branched reticular neurons (see Fig. 30*B*) penetrate deeply from the surrounding reticular formation into the clusters of thickly branched efferent neurons (see Fig. 30*C*) forming the nodes of the switches in the analysers (Zhukova and Leontovich, 1964). Such elements have also been seen there by other researchers (Scheibel and Scheibel, 1955), but they could not show their identity with neurons of the reticular formation.

Reticular neurons are found in the nuclei of the posterior horns of the spinal cord (Fig. 31*A*), in the sensory nuclei of the cranial nerves and switching nuclei of the analysers, located in the medulla oblongata (Fig. 31*B*), and in the formations of the upper subcortex that serve as major transit stations on the pathways transmitting centripetal impulses to the cerebral cortex—in the relay nuclei of the thalamus (Fig. 31*C*), and the lateral and medial geniculate bodies.

The existence of reticular neurons in the analyser-coordination mechanism and analyser systems is not surprising, since they are of essential significance for correlation of the functional connections established between the analysers and the coordination mechanism proper during the organism's reactions to signals being received from its external and internal media.

For an understanding of the complexity of the structure of analysers it is very important to bear in mind that another kind of internuncial element represented by neurons with short axons (or forms transitional to them) (Fig. 32*C* and *D*) has been found in them apart from reticular neurons

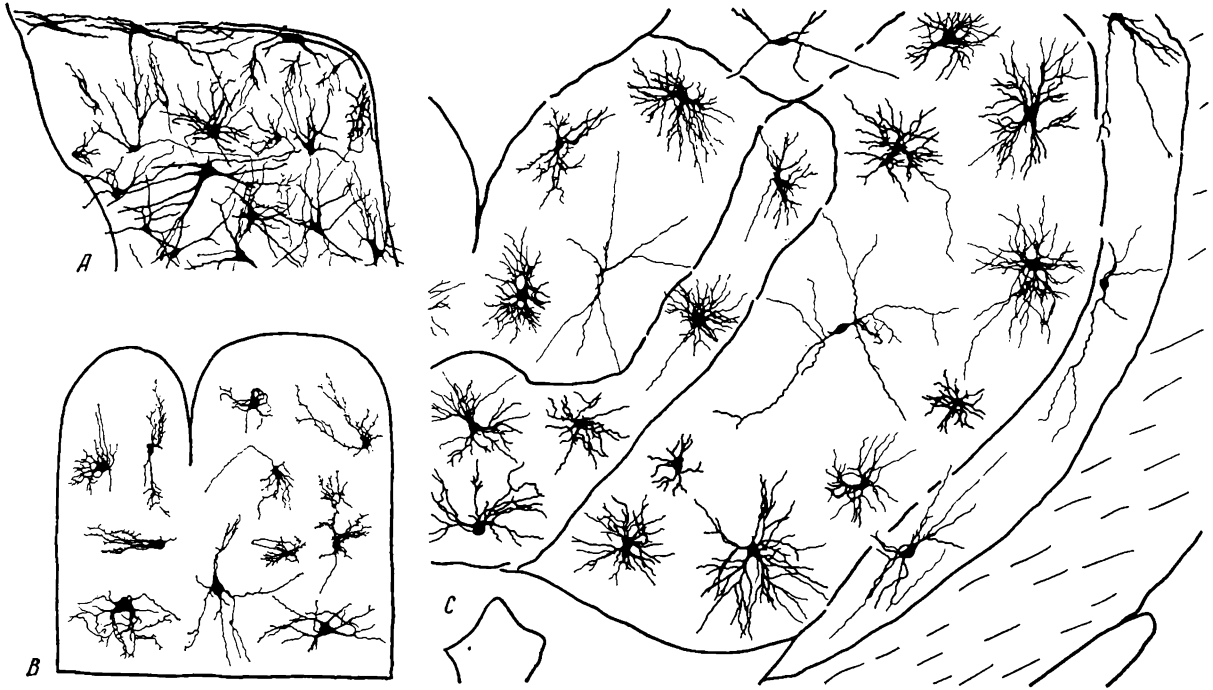


Fig. 31. *A*, posterior horn of spinal cord; *B*, switching nuclei of the cutaneous and kinaesthetic analysers in the medulla oblongata; *C*, switching (relay) nuclei of the same analysers in the thalamus (between-brain). It will be seen that separate rarely branched neurons of reticular form are found among the main mass of thickly branching efferent neurons (*A* and *B*, after Zhukova; *C*, after Leontovich).

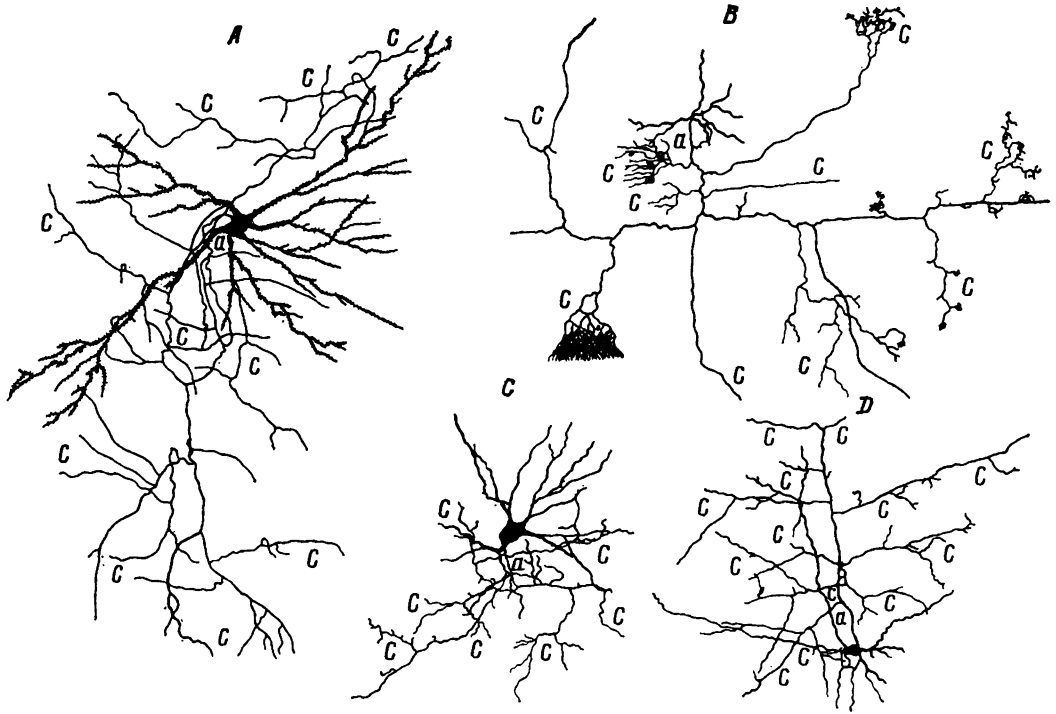
(Fig. 32*A* and *B*). Both kinds are distributed among the main mass of efferent neurons switching centripetal impulses along the analysers.

The chief difference between reticular neurons and those with short axons is as follows. Reticular neurons have more or less long axons with branches distributed along the axis of the CNS, and forming contacts with groups of motor neurons or of other reticular neurons located in the various segments of the spinal cord or at different levels of the brain-stem (see Fig. 32*A* and *B*, and Fig. 15, *rf*). The short axons, as Golgi and Ramon y Cajal noted in their fundamental studies of the neuronal structure of the brain, as a rule, do not pass beyond the confines of a relatively limited part of the grey matter where the cell itself is located; the terminal branchings of short axons are distributed around the bodies and dendrites of neighbouring cells (see Fig. 42*x*—stellate cells with short axons at the level of the fourth layer of the cortex).

The interneuronal connections established by way of internuncial neurons (both those with longer and those with short axons) play a most important role in the joint activity of various groups of efferent neurons; and both kinds of element, in transmitting impulses from afferent fibres to efferent, promote functional unity of the efferent neurons, the terminal branchings of their axons directly contacting the definite groups of efferent neurons involved in carrying out one stage or another of a reflex act (see Fig. 15, *rf*; Fig. 36, *s*).

Neurons with short axons are numerous in the cortical sections of the analyser-coordination mechanism, for example in the cortex of the cerebellum and the cortex of the anterior colliculi which correspond to the optic lobes in lower vertebrates and birds. But neurons with short axons are especially rich and varied in the higher cerebral ends of the analyser systems that form the supra-axial part of the CNS—in the subcortical ganglia of the cerebral hemispheres (Fig. 32*C*) but mainly in the cerebral cortex (the so-called stellate cells—see Figs. 32*D* and 33). There this type of element forms an essential part of the complexly differentiated plexuses of dendrites and axon branchings that penetrate the grey matter of the cortex (Fig. 34).

The branchings of the short axons of stellate cells become particularly complex and fine in the cortex (Fig. 35); and



F i g. 3 2. Various types of internuncial (intermediate or intercalary) neurons; *A*, neuron of reticular form in the posterior horn of the spinal cord (Golgi, 1894); *B*, reticular neuron of the medulla oblongata (Scheibel and Scheibel, 1958); *C*, neuron with short axon from the subcortical ganglia of the cerebral hemispheres (Leontovich, 1952); *D*, neuron with short axon from the cerebral cortex (Poliakov, 1956); *a*, axon of nerve cell; *c*, collaterals of axon.

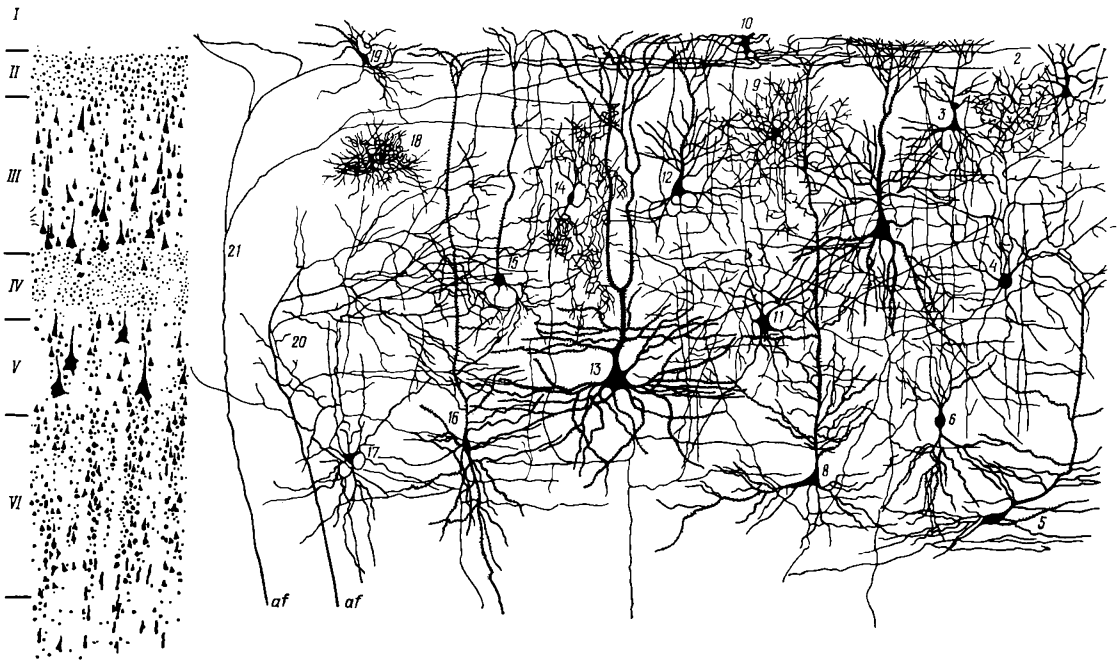
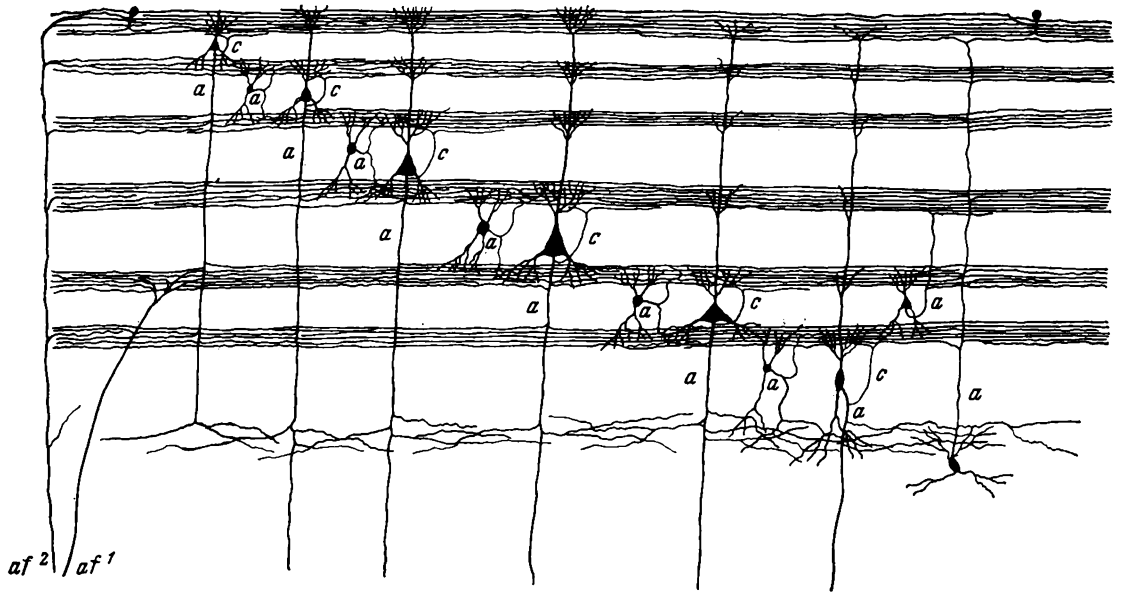
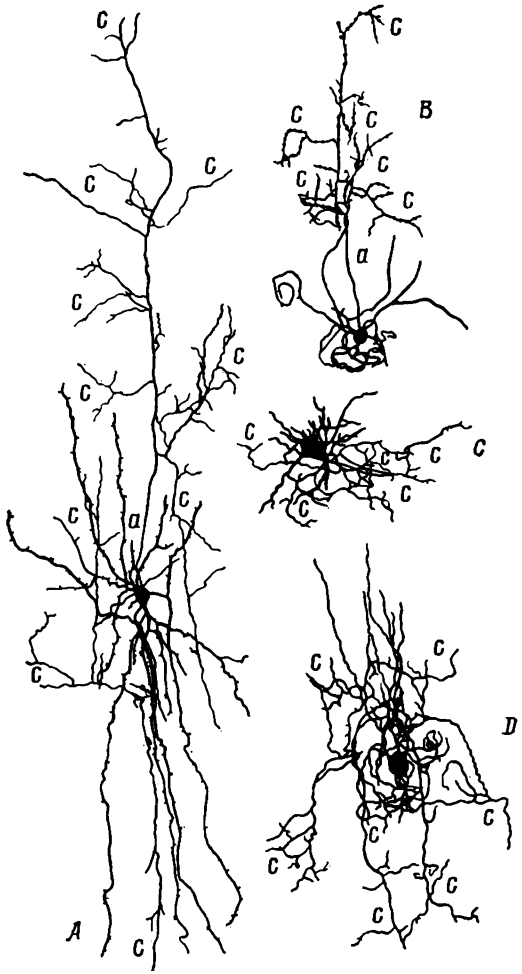


Fig. 33. Map of the neuronal structure of the human brain. On the left are represented the cyto-architectonic layers of the cortex; *af*, projection (*20*), and association (*21*) afferent fibres; *1*, *3*, *5*, *7*, *8*, *12*, *13*, *15*, *16*, efferent neurons with long axons (pyramidal and spindle-shaped cells); *2*, *4*, *6*, *9*, *11*, *14*, *17*, *18*, *19*, internuncial neurons with short axons (stellate cells) (after Poliakov, 1953).



F i g. 3 4. Schematic diagram of the horizontally oriented plexuses penetrating the grey matter of the cortex, formed of branchings of the dendrites and axons of nerve cells. The scheme represents pyramidal neurons with long descending axons and stellate neurons with short axons. The side and recurrent collaterals of long axons and the branchings of short ones are located in contiguous plexuses within the cortex; af^1, afferent projection fibre bearing impulses to the cortex from subcortical switching instances of the analyser systems; af^2, association afferent fibre bearing impulses to a given point from other points in the cortex; *a*, axon of nerve cell; *c*, recurrent collateral of axon of pyramidal cell (Poliakov, 1962).



F i g. 3 5. Various forms of stellate cell with short axons in the cortex. *A*, *B*, stellate cells with ascending axons giving off many side branches; *C*, stellate cell with very fine and fragile axon branchings located close to the cell body forming a partial cover with its dendrite branchings; *D*, stellate cell with axon broken down into a host of very fine and dense terminal branchings oriented in various directions within the grey matter of the cortex; *a*, axon; *c*, collaterals of axons (Poliakov, 1956-61).

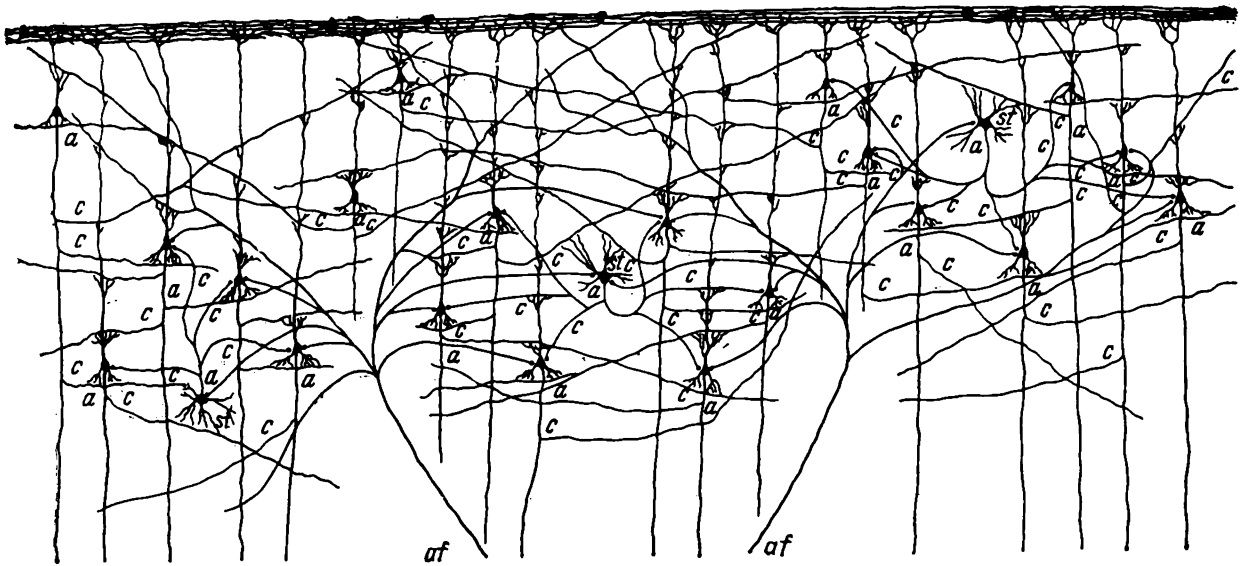


Fig. 36. Elements of the neuronal organization underlying the mobile, functional mosaic of the cortex. The scheme shows centripetal afferent fibres (*af*), entering the cortex from subcortical sections of the analysers and forming numerous contacts with efferent neurons with long axons (pyramidal cells) and with intercalary neurons (cortical stellate cells with short axons) (*st*). Each stellate cell unites a group of pyramidal cells functionally into a microscopic 'combination centre' by the branchings of its short axon; *a*, axons; *c*, collateral branchings of axon (Poliakov, 1961).

as a result a host of microscopic 'combination centres' are differentiated within the grey matter (Fig. 36), which would seem to be the morphological basis of the mobile functional mosaic of excitatory and inhibitory points in the cortex about which Pavlov wrote. Stellate cells with short axons, together with the main mass of efferent neurons, would seem to be the most important structural component of the material basis for the processes of analysis and synthesis and the logical operations performed in the cortex.

We have noted the structural differences between reticular neurons and those with short axons brought about by the peculiarities of the various kinds of interneuronal connection. In addition to them, however, there are also certain similarities of structure in both that make them resemble one another and justify their inclusion in a single general group of internuncial neurons. The facts substantiating this supposition relate mainly to the features of the contacts or synaptic junctions between neurons (see the following section).

It has also been shown by electrophysiological techniques that the neurons that we assign to the general group of internuncial neurons have their own functional characteristics. Their specific feature, as already noted, is their capacity to generate high-frequency, rhythmic discharges in response to a single stimulus—upwards of 1000 impulses a second. This reaction is characteristic of individual reticular neurons in the axial part of the CNS (Kostyuk, 1962), and of intermediate neurons (with short axons) in the cortex. Elements similar in function have also been found in the subcortical formations of the analyser systems.

4. Forms of Contacts and Functional Interconnections between Neurons

In a central nervous system characterized by a great variety of interneuronal connections two main forms of contact junctions between neurons (synapses) can be distinguished. The main means of interneuronal connections are the terminal branchings of the axons that run to the bodies and dendrites of other nerve cells and terminate there in small thickenings of various shape (Fig. 37, *p*, *sp*, *st*; Plate III, *1*, and *2*). These terminal synaptic apparatuses (which we

have observed to develop very early in the embryo) seem to be adapted to direct, unmediated action by one neuron on another.

In the later stages of ontogenesis another kind of contact junctions is formed in connection with the progressive growth of dendrite branchings in addition to the further development and complication of the terminal axon contact apparatuses in the higher cerebral representations of the analysers. This second form of contacts is effected by means of protoplasmic processes on the dendrites, so-called appendages ('spines') (see Plate II *A*, *1*, *2*, *3*, and *7*); dendrite processes with a thickening ('head') at the end are, like the endings of axons, a peculiar kind of specialized synaptic formation. The heads of the appendages not only establish direct contacts with the terminal branches of the axons running to them but also and mainly make tangential contacts with axon branchings and collaterals passing beside them (see Plate III *3*, *4*, and *5*, and Fig. 37)*. This form of contacts (first established by us in preparations stained by silver chrome) has since been confirmed by Gray's electron microscopic studies and other research.

The tangential contacts of axon branchings with dendrite appendages would seem to serve primarily to exert an indirect influence by one neuron on another; impulses addressed to certain neurons influence the functional state of many 'outsiders' in passing by means of these contacts.

Appearing later as they do in ontogenesis (and probably also in phylogenesis) than terminal contacts, tangential contacts can be looked upon as a supplementary to the basic form of interneuronal connections in the CNS represented by terminal contacts. Their emergence was apparently brought about by the further complication in

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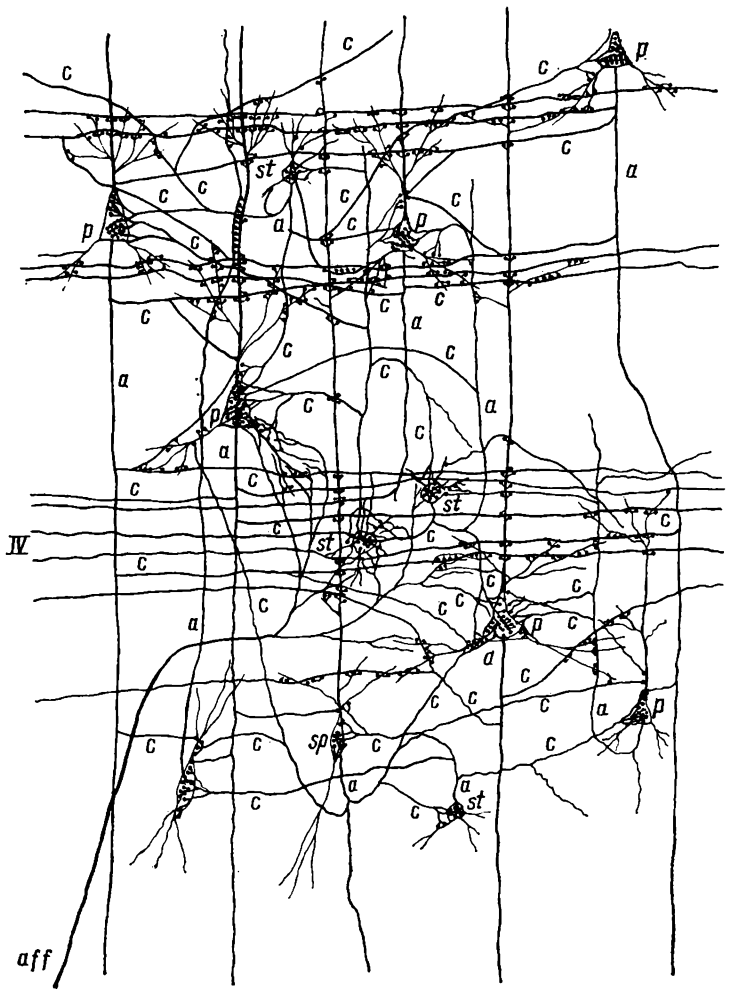
* The contacts of axon branchings with the appendages on dendrites were first noted by us in the cerebral cortex of a man in 1947. Subsequently they were found by co-workers in our laboratory (E. G. Shkolnik-Yarros and T.A. Leontovich) in the cortex and subcortical formations of various animals. The first reference to these contacts was made in Shkolnik-Yarros' paper 'Contribution to the History of Study of the Fine Structure of the Cerebral Cortex' (1950). We ourselves have published detailed description of these formations and an interpretation of their possible functional significance in a number of researches (1953-63).



F i g. 3 7. Forms of contacts or synaptic junctions between neurons in the cerebral cortex differing in functional significance; *aff*, afferent fibre from subcortical sections of the analyser systems whose terminal ramifications make contacts with both efferent and internuncial cortical neurons; *p*, pyramidal cell with long axon; *sp*, spindle-shaped

phylogenesis and ontogenesis of the whole sphere of axon and dendrite ramifications in the most highly organized parts of the CNS.

Terminal and tangential contacts have, we would suggest, quite different significance for the functional state of a neuron. The transfer of the affected neuron from one basic functional state to another (from a state of excitation to one of inhibition, and *vice versa*) would seem to depend in the highest degree upon terminal contacts specialized to exert a direct influence on other neurons. Indirect side influences (realized by way of the tangential type of contact) on the contrary would seem to have only subsidiary significance in the interactions of neurons, facilitating or hindering the transition of a neuron from one basic functional state to another. Thus the general state of each individual neuron at one moment or other of the performance of a reflex act is determined by the interaction of direct and indirect influences from many other neurons, in which the dendrite apparatus (in which the main mass of tangential contacts is concentrated) probably plays the role of a fine modulator of the functional state imparted to the neuron. With the development of dendrite ramifications the functional plasticity and reactivity of neurons is correspondingly raised, i.e. their 'responsiveness' to changes of state in other neurons.

To understand the character of the influences that neurons exert on one another in the course of the joint activity, it is important to elucidate the relationship in the distribution of terminal and tangential contacts at the surface of the cell bodies and the dendrites of various neur-

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cell with long axon; *sp*[1], spindle-shaped cell with ascending axon; *st*, stellate cell with short axon; *a*, axon; *c*, collateral branching of axon. It can be seen that the ramifications of axons run to the bodies and dendrites of nerve cells, forming terminal synapses with them. The 'nests'or 'baskets' formed around the bodies of pyramidal and stellate cells by the terminal branchings of the short axons of other stellate cells deserve notice. In addition to terminal contacts, tangential contacts can also be seen, formed between axon collateralls and the appendages on the dendrites of nerve cells. These contacts are particularly well expressed along horizontal nerve fibres (Poliakov, 1961).

ons. The structure, distribution on dendrites, and number of appendages differ, as we have established, among neurons of various functional purpose.

In cortical sectors both of the analyser-coordination mechanism (cerebellum) and especially of the analyser systems, the dendrite ramifications of efferent neurons with long axons are covered by numerous, close packed, short appendages; the body of the nerve cell itself, on the contrary, and the initial sections of the stems of its dendrites, as a rule have no appendages. In the cerebral cortex the most typical elements of this kind are the pyramidal cells (see Plate II, *1* and *2*). A like structure is also found in the long-axon efferent neurons of the most highly organized sections of the subcortical ganglia of the cerebral hemispheres (see Plate II, *A*, *3*).

As neurohistological research has shown, the cell body of efferent neurons and the initial sections of its dendrites, which are without appendages, is the place where terminal contacts are mainly made. On that basis it can be supposed that the basic functional state (excitation or inhibition) of efferent neurons is determined in the first place by impulses acting on the central part of its perceptive surface. On the other hand the strongly developed dendrite ramifications of efferent neuron, with their very numerous appendages, can be regarded as the field of application of supplementary, indirect influences on its state. Efferent cortical neurons are most sensitive consequently to all kinds of impulses reaching the cortex from various near and distant sources and circulating in every direction within the grey matter.

The short-axon cells of the cortex and subcortical ganglia (see Fig. 32*C* and *D*, and Fig. 35), which are specialized for another kind of interneuronal connections, are characterized either by an absence of appendages on their dendrites (Plate II, *4*), or have only rare elongated offshoots (Plate II, *5*). The circumstance that the dendrites of the reticular neurons of the brain-stem and spinal cord also have rare, widely separated elongated appendages (Plate II, *7*; see also Fig. 30*B*) deserves attention; the appendages bear a certain resemblance in this respect to the short-axon cells of the cortex and subcortical ganglia of the cerebral hemispheres. The existence of elements of similarity in the fine structure of both short-axon and reticular neurons also gives us

grounds for classing both in a single general group of functionally related internuncial neurons.

The physiological significance of the differences noted above in the structure of the dendrites of efferent and internuncial neurons (taken to include both reticular and short-axon cells) we see as the following. The efferent neurons of the cortex and subcortical ganglia of the cerebral hemispheres (and also the cortical sections of the analyser-coordination mechanism located along the axis of the CNS), with their strongly developed dendrite branchings covered with numerous appendages, are evidently powerful collectors both of impulses adressed directly to them and of those influencing their functional state indirectly (by way of tangential contacts with appendages).

On the contrary, internuncial neurons (both those with short axons and reticular ones with more or less long axons) that have only rare appendages on their dendrites (or are quite without them) are, it would seem, the places where mainly terminal synapses are effected, i.e. are basically adapted for establishing terminal contacts with other neurons. The characteristic elongated form of the rare appendages on their dendrites would seem to be due to the fact that internuncial neurons form only relatively few or even single contacts of a tangential type in addition to their many terminal ones. That proposition can be taken to apply, in particular, to neurons of the reticular formation; Kositsyn (1962) has succeeded in tracing numerous terminal synapses covering their dendrites for a considerable distance. Because of this structural peculiarity the whole perceptive surface of cells with short axons, and of reticular neurons, can be likened to the central part of an efferent neuron. The elements of both types are specialized, it would seem, mainly for the convergence of impulses that exert a direct influence on their functional state. On the other hand they themselves are also predominantly sources of direct influences on other neurons. In support of that last statement we would cite our own finding that the axons of stellate cells of the cortex form very fine interlacings in the shape of 'nests' or 'baskets' (Fig. 37, *p*) through their terminal ramifications on the bodies, and initial sections of the dendrites, of efferent neurons (pyramidal cells); from which it can be concluded that stellate cells are in a position to act directly on the efferent neurons that they

unite functionally for joint activity. The scarcity of appendages on the dendrites of internuncial neurons can be taken as an indication that the latter are apparently specialized to establish selective, differentiated contacts with afferent fibres and other neurons. Being concentrators and distributors of direct influences, the internuncial elements of various kind would seem to have an essential role in determining the functional state (excitation or inhibition) of efferent neurons.

These features of the interneuronal connections established by means of internuncial neurons accord with our views on the special role of these elements in processes of fine coordination, simultaneously and consecutively switching on the action of some groups of efferent neurons and switching off others.

CHAPTER IV

THE BASIC SCHEME OF SWITCHES IN THE NEURONAL NETWORK

1. The Central Switching Apparatus in Analysers

In the preceding chapter we presented factual material relating to the origin and complication of neuronal networks, and expressed certain views about them. We also surveyed the elements that make up the coordination mechanism and the analysers, and emphasized the very important role of internuncial (intermediate or intercalary) neurons in their structure. In this section and those that follow we shall deal in more detail with the organizational features of the neuronal switches in the analysers, and try to determine more exactly the place of internuncial neurons in the whole system.

How have these elements evolved and on what topographical plan are their interaction with other neurons built?

In our efforts to find the answers to those questions, which are of essential importance for understanding the working of the whole design, we returned to the problem of the origin of ordered reflex activity in the organism.

As has already been indicated, it must be considered a characteristic feature of a reflex act of any degree of complexity that it is always effected in a coordinated manner in normal conditions, and that applies in equal measure to all stages of the performance of a reflex act. Elucidation of the neuronal mechanisms that ensure the activity of the analysers, especially of their higher and most complexly organized sections, is of special value for answering the questions posed above.

On the basis of our hypothesis of the origin of the neuronal

networks (see Fig. 27) we have drawn up a scheme of the formation of an elementary coordination apparatus, comprising a minimum of interacting elements (altogether two receptor and two effector points) (Fig. 38*A*). (Obviously, with only one receptor and one effector there is generally no biological need to create any kind of special coordination instrument.)

As can be seen from Fig. 38*B*, an elementary coordination apparatus will inevitably include, at the stage when the neuronal network becomes differentiated, not only lines of direct transmission of impulses from receptors to effectors but also the prototype of an internuncial neuron (*n*), inasmuch as this element (which corresponds in a developed coordination mechanism to a reticular neuron) is located between the central section of both reflex arcs (compare with Fig. 11*B*, *3*).

Turning to the problem of the origin of a switching apparatus in analysers, we take as our point of departure our earlier proposition that analysers evolved as a further elaboration of the functional potentials inherent in the coordination mechanism itself from the moment it came into being. The reorganization of the system of switches in the analysers, in comparison with that of the coordination mechanism (see Fig. 11*B*), we understand as an **augmentation** of the elementary coordination device (an elem-

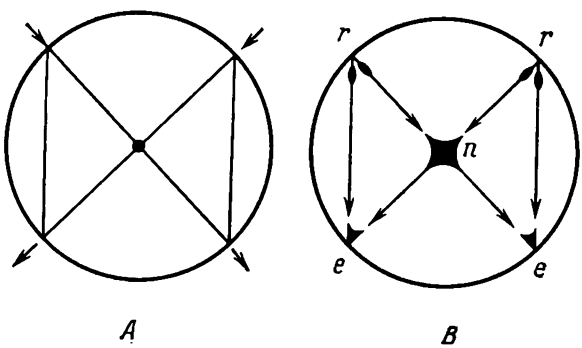
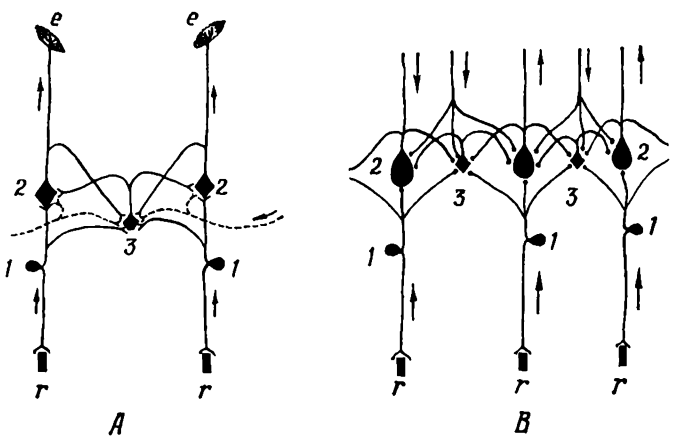


Fig. 38. Schemes of the origin of an elementary coordination apparatus; *A*, simplest combination of interconnections between two receptor and two effector points; *B*, elementary bit of a neuronal network consisting of two receptors (*r*), two effectors (*e*), and an internuncial neuron (*n*).

entary unit of the coordination mechanism) in connection with the colossal complication of the signalization that is transmitted by an analyser.

The process can be represented visually if we alter the diagram of the elementary coordination device (see Fig. 11*B*) in such a way that the distribution of its elements will be oriented in the same ascending direction (Fig. 39*A*) as the neurons in the switching nodes of the analysers (Fig. 39*B*). By making such an alteration we see that there are also internuncial neurons with short axons located in the analysers **between** the efferent neurons with long axons in the parallel chains transmitting impulses; in that



F i g. 3 9. *A*, transformed scheme of an elementary coordination apparatus oriented in the same direction (see *B* bellow) as the chains of neuronal switches in the analysers (compare with Fig. 11*B*); the designations and broken lines in *A* correspond to those in Fig. 11*B*; *B*, scheme of the structure of the neuronal switches in the analyser (augmented elementary coordination apparatus); *r*, receptor; (*1*) peripheral sensory neuron transmitting centripetal (afferent) impulses from the receptor both to an efferent neuron with long axon (*2*) and to internuncial neurons with short axons (*3*) included in the switching node. In addition to ascending (centripetal) conductors (arrows pointing upward), descending (centrifugal) conductors are also indicated (arrows pointing down), which correspond to the broken lines in *A*. As can be seen in *B* the general distribution plan of the terminal ramifications on efferent and internuncial neurons is the same for both centripetal and centrifugal connections.

way a basic likeness can be established between the distribution of that type of element in the analysers and of the internuncial neurons of the reticular formation in the reflex arcs of the spinal cord and brain-stem.

This reorganization would seem to be conditioned by the following factor. In the coordination mechanism such an apparatus was formed directly between the input and output of the CNS; in the analysers it appears to be 'built' into the chains of consecutive transmission of centripetal impulses from the lower to higher levels of the CNS. The evolution of neurons with short axons in the analysers is an essential morphological index of the finely and complexly differentiated processes for switching impulses in the analyser-coordination mechanism, and particularly in the analyser systems. It can be considered that the internuncial neurons located in the analysers in the zone of synaptic junctions between efferent neurons have a very important role in transforming 'logic treatment' and 'filtering' information, which makes it possible to single out the really significant signals.

Further complication of the whole scheme of switches in the analysers has been brought about by the development in them, alongside the apparatus of ascending centripetal transmission of nerve impulses, of an apparatus of descending, centrifugal transmission, represented by the terminal branchings of the axons of neurons lying higher and contacting neurons of the lower levels (Fig. 39*B*).

The same general scheme of convergence of both ascending and descending conductors (see Fig. 39*B*) on the efferent and internuncial (short-axon) neurons applies in the analyser, it can be suggested, as in the analogous interneuronal relations in the elementary coordination device (see Fig. 11*B*). The efferent and internuncial neurons of any switching node in an analyser are thus under the constant influence of opposite streams of impulses from above and below; and it can be thought that the tuning and self-tuning of the analysers to the effects of stimulation (which is an essential component of the active concentration of attention on a studied object) is performed by means of this mechanism.

We are still far from a clear understanding of the physiological nature of the complex coordination processes taking place in the cerebral parts of the analysers and ensuring

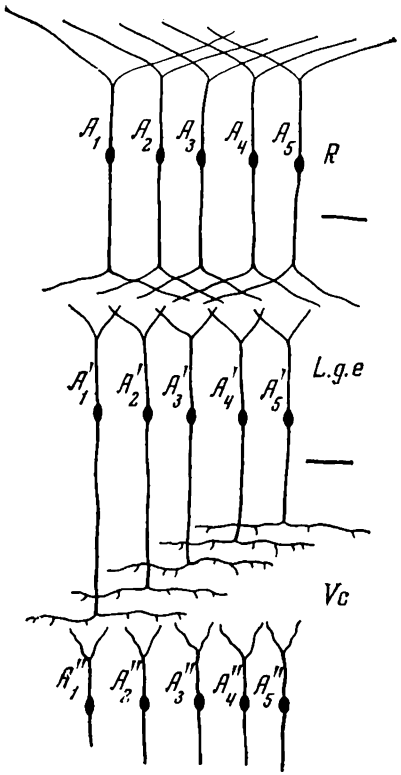


Fig. 40. Lorente de Nó's scheme (1934) showing partial overlapping of the processes of neurons in the switching instances of the system of visual analyser A_1—A_5, neurons of the retina (R); A'_1—A'_5, neurons of the subcortical switching node (L.g.b., lateral geniculate body), A''_1—A''_5, neurons of the visual cortex (v.c.)

the adequacy of their response activity to external stimulation. It seems obvious, however, that these processes there are in principle underlain by the same reciprocal interrelations of excitation and inhibition in functionally conjugated groups of neurons as in more elementary coordination devices. Ukhtomsky stressed that the most varied combinations (constellations) of neurons located at different levels of the CNS can be drawn into reciprocal relations. That suggestion enables us to explain certain phenomena observed in Jung's fine electrophysiological experiments (1958). At different moments of the action of stimuli definite groups of neurons in the various links of the analysers have been observed to be reacting selectively (by excitation or inhibition) to switching on and switching off, and to changes in the action of stimuli ('on' and 'off' effects).

In our own findings relating to the cortex of the human brain internuncial neurons (stellate cells with short axons) often display a tendency to lie between groups of efferent neurons with long axons represented by pyramidal cells (see Fig. 36). This feature may indicate that these stellate cells functionally unite the groups of efferent neurons between which reciprocal dynamic relations are thus established; such a form of interconnections between pyramidal and stellate cells corresponds to the topographical relationship between efferent and internuncial neurons in the coordination mechanism and in the subcortical switching instances of the analysers presented in our diagrams (Fig. 39*A* and *B*).

We shall now touch briefly on the mechanism proposed by us for the origin in the analysers of internuncial neurons with short axons.

A fundamental feature of the construction of analysers is the regularity formulated as the rule of partial mutual overlapping of neurons (Lorente de Nó, 1934; see Fig. 40). Morphologically this arrangement is characterized by the fact that in all the switching formations of the CNS the terminal branchings of one and the same afferent nerve fibre run directly to several efferent neurons. Thus the endings of several nerve fibres cross over one another, i.e. overlap. In that way one and the same efferent neuron establishes contacts with several neighbouring afferent fibres, i.e. comes under the influence of impulses reaching it along different nerve conductors. It is important to note that the principle of mutual overlapping is already clearly expressed at the level of the junction of neurons with receptors. Otelin's recent research (1961) has shown that definite receptor formations of the skin (the Vater-Pacini sensory corpuscles) each as a rule receive the endings of several peripheral nerve fibres (poly-axon receptors in Otelin's terminology).

We consider this regularity in the structural organization of switches as a special case of the universal scheme of mutually intersecting pathways uniting all receptors with all effectors postulated by us (see Chapter III and Fig. 27). In fact it is also determinant for Lorente de Nó's rule that every neuron in a switching node serves as a point of convergence and divergence of the impulses being transmitted along the neuronal chains.

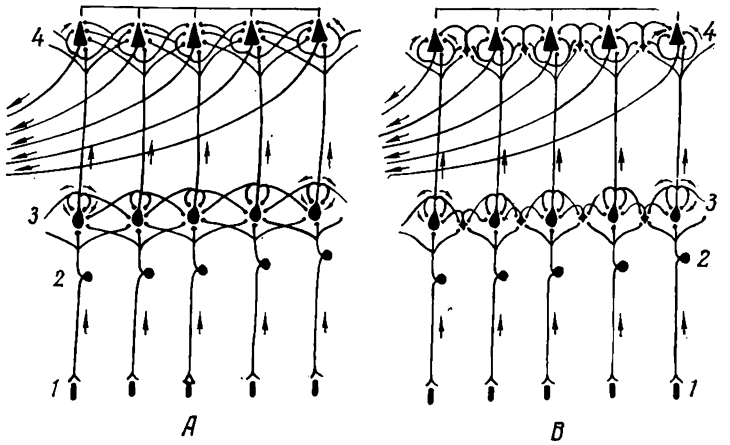
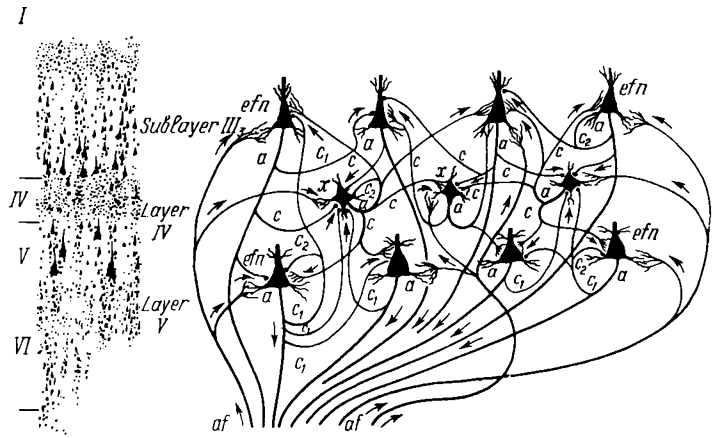


Fig. 41. Schemes of the switching apparatus corresponding to lower (*A*) and higher (*B*) levels of development of analysers. In *B*, which is more complicated (in relation to *A*), internuncial neurons with short axons, formed at the mutual intersections of terminal ramifications and recurrent collaterals, are shown in addition to the elements represented in *A*. *1*, receptors; *2*, peripheral sensory neurons; *3*, subcortical section of the analyser; *4*, cortical zone of the analyser. Efferent neurons with long axons are represented. In *A* only the mutual overlapping of the end ramifications of afferent fibres and the recurrent collaterals of the long axons of efferent neurons are shown, recurrent collaterals coming back onto the body of their own neuron are also represented.

In the scheme in Fig. 41 internuncial neurons with short axons arise in accordance with our conception of the physiological mechanism of the origin of neurons at points of crossing and mutual intersection of the streams of impulses transmitted by the terminal ramifications of afferent fibres and recurrent collaterals of the axons of efferent switching neurons (as described earlier in Chapter III, section 1) (compare *A* and *B* in Fig. 41).

Working on this hypothesis, it is possible, in particular, to give a rational explanation of the origin of the inner granular layer of the cortex (fourth layer—see Fig. 42). This layer, which plays a most essential role in the switching of impulses that reach the cortex from the subcortical sections of the analysers, contains an accumulation of many so-called granular cells of stellate and pyramidal



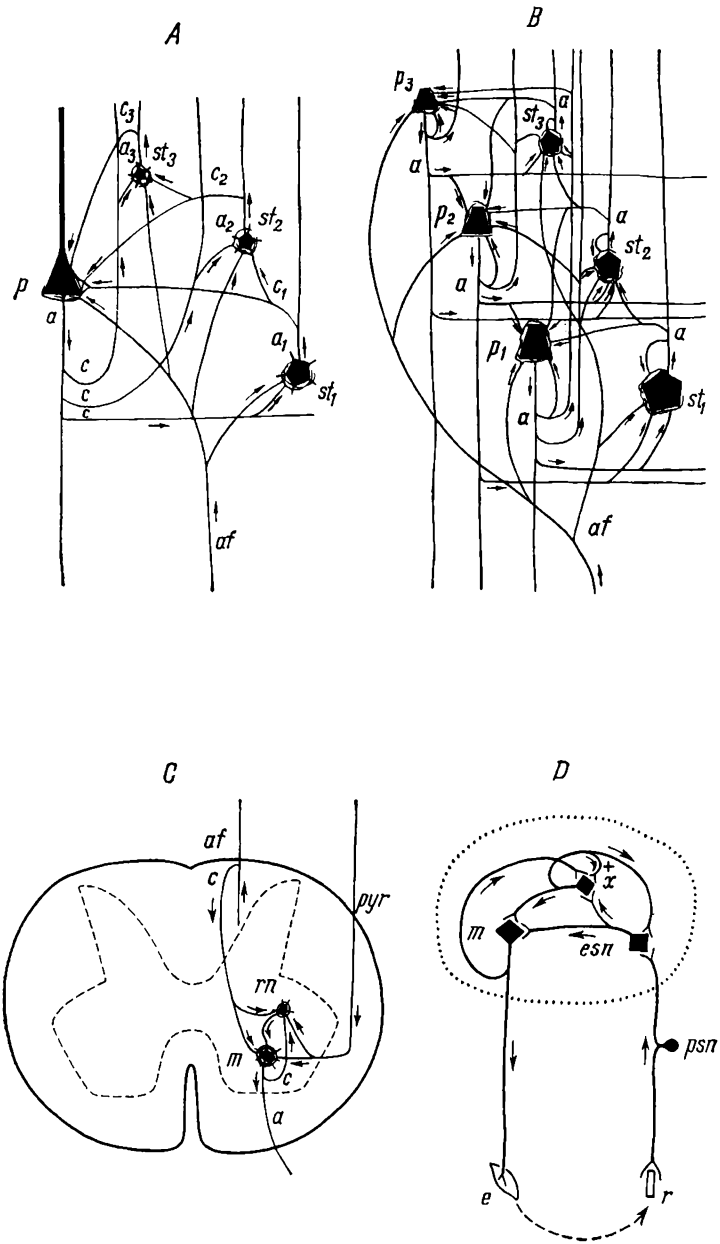
F i g. 4 2. Semi-schematic drawing of interneuronal connections in the cortex at the levels of sub-layer III_3, and layers *IV* and *V*. On the left are shown the cyto-architectonic layers of the cortex; *af*, afferent fibres from subcortical switching stations of the analyser systems; *efn*, pyramidal cells with long axons of sublayer III_3 and layer *V*; *x*, stellate cells with short axons of layer *IV*; *a*, axons; *c*, axon collaterals; c_1, recurrent collaterals of the axons of pyramidal cells; c_2, collaterals doubling back on their own neuron. Arrows indicate the movement of nervous impulses taking part in the closing circles of feed-back connections and mutual excitation of neurons. To simplify the diagram only a few of the actual number of connections between the afferent fibres, and pyramidal and stellate cells of the cortex are represented.

form with short axons spreading on all sides or bending upward. The ramifications of the short axons of the various cells are closely interlaced and overlap many times. At this level where assemblages of the short-axon internuncial neurons of the fourth cortical layer are concentrated, there is also a dense plexus of the mutually overlapping terminal ramifications of afferent fibres coming from subcortical formations of the brain. We would note, in passing, that these afferent fibres, in accordance with our scheme, establish contact not only with the stellate type of internuncial neurons but also with efferent neurons with long axons, and pyramidal cells of layers III (III_3) and V of the cortex (see Fig. 37).

The general scheme shown in Fig. 41 is, of course, an abstraction that does not reflect the full complexity of the real relations between afferent, efferent, and internuncial neurons in the various formations of the CNS at the different stages of individual and species development. In the evolution of vertebrates structural specialization of the chains of neuronal switches develops in diverse directions. Depending on the functional specialization of the appropriate formations the process is expressed in a reinforcement of certain morphological signs and the simultaneous weakening of others. Thus, in the observations of Zhukova, Leontovich, and Shkolnik-Yarros, the subcortical switching nodes in the analyser systems (so-called relay-nuclei) adapted to rapid transmission from the periphery to the cortex of precise signalling with a clearly expressed local sign, and organized on the principle of somatotopic projection, have in particular weak developed collaterals of the long axons of efferent neurons. Our own findings are that the collateral branchings of these axons, and the ramifications of the short axons of internuncial neurons, are very greatly developed in formations with a cortical type of structure and are specialized to perform the most finely differentiated and most complexly integrated forms of treatment of switched signals. A similar feature is also found in the structure of the phylogenetically new sections of the subcortical ganglia of the cerebral hemispheres, which are developed in ontogenesis and phylogenesis from the same formations of the end-brain as the fully developed cortical formations; and which reveal a basic likeness with the latter in several features of the structure of their neurons

2. Central Nervous Apparatuses for Perception and Imprinting

One of the features most characteristic of the construction of the switching formations of analysers is the creation of maximum physiological conditions favouring imprinting of the action of stimuli. As is indicated by the scheme (Fig. 43) the mutual articulations among all the switching elements are so built as to ensure [in accordance with views of Forbes (1922), Lorente de Nó (1937) and others, on closed interneuronal circuits] protracted circulation of impulses across their switching points and constantly renewed


A
B
C
D
p
a
c
c_3
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af
p_3
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pyr
rn
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mutual excitation of the neurons exchanging impulses. In that way long retention in latent form of the traces of excitation becomes possible during their transmission along analysers, as has been demonstrated by current researches in the registration of potentials at the various points where impulses are switched.

Much more complex is the anatomical, physiological mechanism found in the highly organized cortical formations of the cerebral hemispheres that appear last in evolution (Fig. 43*A* and *B*), which incorporates the stellate, short-axon internuncial neurons as an essential component. The stellate cells forming part of the complex constellations of efferent neurons in the cortex, working in conjunction with the subcortical apparatuses, would seem to have an important function in imprinting the excitation reaching the cortex, and also in the processes by which differentiated sensations and perceptions of objects in the external world are formed and reproduced.

The latest improvement in the mechanism of mutual excitation of neurons as regards even finer functional diffe-

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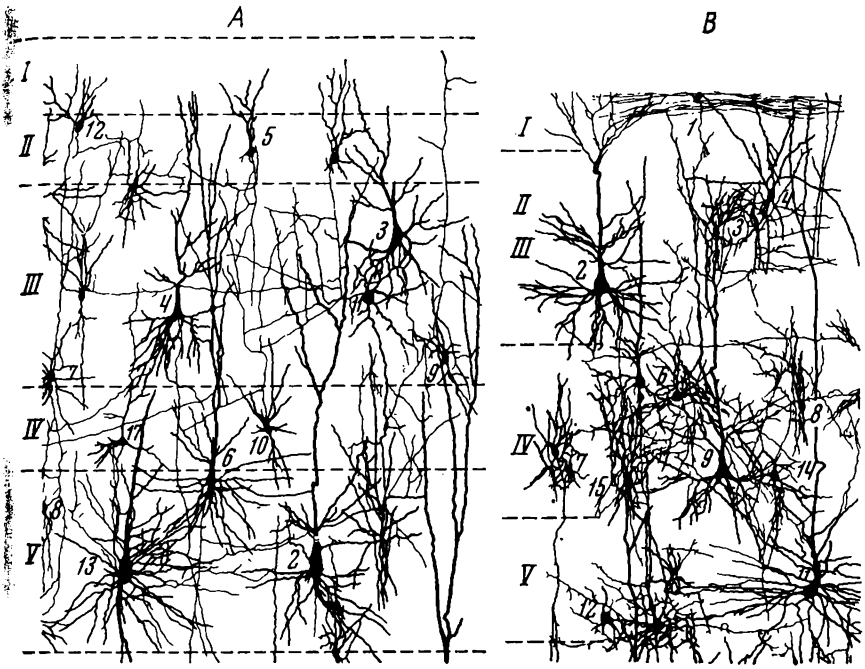
F i g. 4 3. *A* and *B*. Schemes of the interconnections between afferent fibre (*af*), pyramidal cell (*p*), and stellate cells (st_1, st_2, st_3), underlying the closed circulation of impulses in the cortex, *B* represents a more complicated scheme than *A* and illustrates in principle the functional interrelation between the three elements. Attention is drawn to the recurrent axon collaterals by means of which a neuron establishes contact 'with itself' (the mechanism of self-excitation of neurons): *a*, long axons of pyramidal cells; a_1, a_2, a_3, short axons of stellate cells; *c*, c_1, c_2, c_3, axon collaterals; p_1, p_2, p_3, pyramidal cells; st_1, st_2, st_3, stellate cells. Arrows indicate the direction of circulation within the cortex of nervous impulses reaching it along afferent fibres and leaving it by way of the long descending axons of efferent neurons (*n*). (After Poliakov, 1953.) *C*. Scheme of the closed circulation of impulses in the reflex centres of the spinal cord; *af*, afferent fibre conducting centripetal impulses from receptors; *pyr*, fibre of the pyramidal tract conducting centrifugal impulses from the cortex; *m*, effector (motor) neuron; *rn*, internuncial (reticular) neuron; *a*, axon; *c*, axon collateral. *D*, 'Modernized' scheme of a reflex arc, indicating the place of internuncial neuron (*x*) in it, and the character of the interconnections between the internuncial neuron and the other neurons in the arc. The diagram enables one to judge the special significance of this element in closing the feed-back circuit and in effecting circulation of impulses within the central section of the reflex arc during their progressive transmission from receptors (*r*) to effectors (*e*); *psn*, peripheral sensory neuron; *esn*, efferent switching neuron; *m*, effector neuron.

rentiation is the formation of a special apparatus of **self-excitation** of individual neurons. The anatomical basis of this—as we have in fact established for the cerebral cortex—is the recurrent collaterals of axons that terminate on the body and dendrites of one and the same nerve cell (see Figs. 41*B*, 42, and 43*B*). Beritashvili (1963) attaches special significance to these details of the construction of the cortical ends of analysers, and particularly to the stellate cells of the cortex with overlapping ramifications of their dendrites and axons, and has named similar elements as arachnoid cells (see Fig. 35*B*).

For an understanding of the functional significance of stellate cells in the complex processes of the perception, accumulation, and imprinting of excitation and its traces in the cerebral cortex, Popova's research presents great interest. In her work she attempted to compare the character of the motion and interaction of the nervous processes evoked by the technique of conditioned reflexes with the differences in neuronal structure in the systems of the visual and auditory analysers. From the analysis made it was concluded that there was a definite correlation between structure and function. Her work showed clearly that retention of trace processes from conditioned stimuli was longer, the length of the latent period longer, and the nervous processes less mobile in the visual analyser than in the auditory.

The physiological indicators concerned are connected with fine features of the structure of the cortical ends of both analysers, and especially with the differences in structure and distribution of stellate cells in the visual and auditory cortex (Fig. 44). According to the work of Shkolnik-Yarros (see Fig. 44*B*), stellate cells are concentrated thickly in the central visual field of the cortex, are very numerous there, and form fine, dense axon plexuses. In the auditory fields (see Fig. 44*A*) their short axons form much more dispersed and rarely distributed branchings; there are many fewer stellate cells. Thus an impulse passes through a much greater number of switches in the visual cortex than in the auditory; consequently conditions are created there favouring longer conduction and retention of nervous impulses.

These features of the organization adapted to imprinting the diverse external and internal signalling received in



F i g. 4 4. Neuronal structure in the auditory (*A*) and visual (*B*) fields of a canine cortex (fields T_3 and O_1 in Adrianov's and Mehring's cyto-architectonic map). Comparison of *A* and *B* shows that stellate cells of the auditory cortex (*A—7, 8, 9, 10, 11*) are relatively fewer in number and have many rarely branching processes than those in the visual cortex (*B—3, 6, 7, 8, 14, 15*), whose processes form a very fine and dense branchings in the grey matter. (Cortical layers are numbered on the left.) (*A*, after Popova, 1960; *B*, after Shkolnik-Yarros, 1954).

the brain would seem to be directly related to the basic problem of the orientation and reflex movement of the organism in space and time. Animals and men are not only able to perceive events currently happening around and within them and react to them, but also have the 'gift' of latently accumulating impressions of those events. The organism may also not make direct motor responses to stimulation, but preserve traces of it, and of the reactions caused by it, as memory images of past events and as a means of accumulating experience that is used in the strategy and tactics of future conduct. The associations of

psychic phenomena experienced by man have in their basis the real connections of the physiological processes taking place in the appropriate structures of the cerebral cortex and related to the complex spatial-temporal integrations realized there.

Taking the general scheme of the organization of neuronal switches given in Fig. 41*B*, a different specialization of its elements can be suggested for reflex reflection by the organism of events taking place in space and time. Special features can be distinguished adapted on the one hand to effecting the organism's reactions, directed outward to objects in the space around it, and on the other hand to ensuring latent continuity in time of psychic activity.

A structure consisting of chains of neuronal switches oriented along an analyser and joining various points on the perceiving surface with synonymous ones in its cortical end on the principle of geometric correspondence (Fig. 45*A*) is most suitable for exact reflection of the spatial relations of things and phenomena. Such a design finds its most marked expression in the so-called somatotopical 'point for point' projection (see also Fig. 53).

As regards the reflection and retention in the memory of sequence of events occurring in time, that function is apparently connected with another feature of the whole design. Current ideas of the finest structure of the interneuronal connections in the switching instances of analysers (see Fig. 43) give us grounds to consider that the main material substratum of the process is precisely those groups of neurons that are specialized to keep up a long, latent circulation of nervous impulses in the closed circuits of interneuronal connections (Fig. 45*B*). The initial scheme of the 'network' or 'lattice' of switches in an analyser system given in Fig. 41*B* may be taken as the prototype of the apparatus in the brain by which real space-time unity in the material world is reflected.

3. Structural Basis of Functional Localization in the Cortex

The nineteenth century physiologist Munk compared the cerebral cortex with a geographical map on which were located numerous clearly delimited 'provinces' corresponding exactly to the sense organs and motor apparatuses of

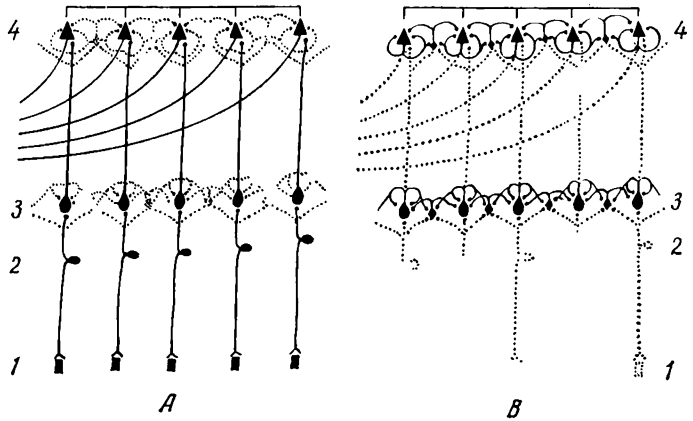


Fig. 45. Diagrams of the two aspects of neuronal organization considered by us to be the morphological basis of reflex reflection of (*A*) spatial and (*B*) temporal relations by the organism. Elements that have a dominant significance in the corresponding form of reflex activity are printed in black, while those that play the part of a subsidiary background to the activity of the leading neuron complexes are represented by dotted lines. The diagrams are explained in the text.

the body. In higher developed mammals there is a fine division of the cortex into regions, sub-regions, fields, and sub-fields differing in their architectonics, resulting from the fact that the cortical representation of the systems of the different analysers (we have in mind the formations of the fully developed neocortex) is an involved complex made up of several sections differing in structure and functional significance. The system of each analyser—visual, auditory, cutaneous, and kinaesthetic—is represented in the cortex by its own special territory, peculiar to it, a corresponding region (Plate V*A* and *B*; Fig. 46*A* and *B*) concerned with the finest analysis and most complex synthesis of stimuli perceived by its peripheral end.

Pavlov called these regions the nuclear zones of the analysers. His view of them has been confirmed by much morphological and physiological research. Thus Lashley's experiments (1960) in isolating the visual zone of the cortex of rats from all its connections with other cortical regions had no effect on the animal's behaviour regulated by

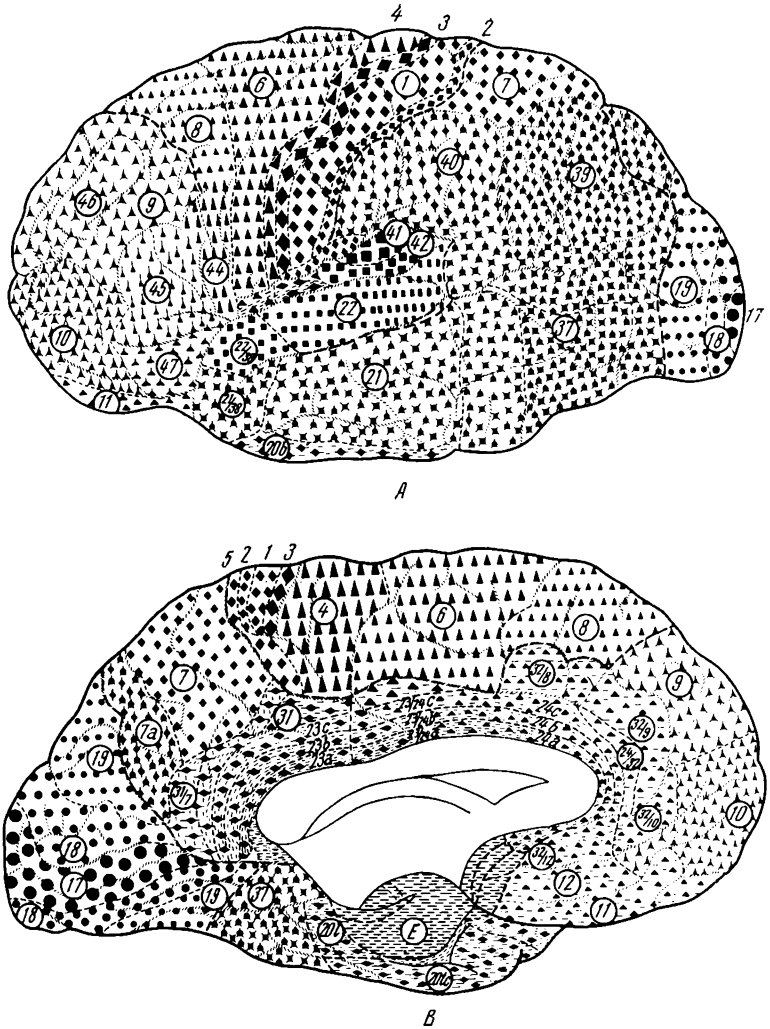


Fig. 46. Diagrams of the topographical interrelations of the fields of the cortical zones of the analyser systems and of their zones of overlapping on the lateral (*A*) and medial (*B*) surfaces of the cerebral hemispheres of man. Figures indicate the same cytoarchitectonic fields as in Plate V. The cortical zone of each analyser system is distinguished from the others by symbols as follows: visual by circles; auditory by squares; cutaneous-kinaesthetic (zone of bodily sensation) by diamonds, motor by triangles. Their boundaries are demarcated

visual stimulation. Monkeys do not lose their ability to distinguish the colour, brightness, and shape of objects.

Within each cortical (nuclear) zone there are a number of specialized fields that are linked with the peripheral receptive surface of the analyser system (the corresponding sense organ) through a varying number of switches in the upper and lower subcortex (see Plate VI and Fig. 53).

In the course of mammalian evolution (when the neocortex first develops) special sections (the central fields of cortical zones of analyser) become differentiated within the specialized regions of the neocortex (visual, auditory, cutaneous, and kinaesthetic) (fields 17, 41, 3, and 4 in Plate V and Fig. 46). Because of their structural and functional features these fields are adapted for the maximum detailed breaking down of individual stimuli and are thus the material substratum in man of finely differentiated sensations.

The cortical formations of which we speak are linked with the sense organs through a minimum number of switches in the sub-cortical sections of the analyser systems (see Plate VI and Fig. 53). It is important to note that these connections are mainly built on the principle of

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by heavy broken lines, and the boundaries of the separate fields by fine broken lines. The central field of each zone is indicated by the largest symbols, the secondary (peripheral) field about it by smaller symbols, and the most peripheral field of the zone by the smallest symbols. The zones where the visual, auditory, and cutaneous-kinaesthetic analysers overlap (the fields of the superior and inferior parietal regions and temporal-parietal-occipital sub-region) are represented by a mixture of the symbols of the corresponding analysers. The fields of the frontal region are represented by the same symbols as the motor zone but less closely spaced. The motor-speech (fields 44 and 45) and auditory-speech (the posterior part of field 22) sectors are distinguished by alterations of the shape of the symbols of the related cortical zones. The boundary regions of the neocortex, bordering on the formations of the intermediate cortex, archicortex and palaeocortex—the limbic (fields 23 and 24) and the insular regions hidden in the depth of the Sylvian aqueduct—and the fields of the neocortex functionally related to them, and located on the basal and medial surfaces of the frontal and temporal lobes (fields 47, 11, 12, and 20), are denoted by horizontal hatching and flattened symbols among the hatching; the density of the hatching increases with proximity to the formations of the intermediate cortex, archi- and palaeocortex (to use Filimonov's classification), which are represented by heavier horizontal lines (after Poliakov, 1961).

exact spatial correspondence of each point on the perceiving surface with a definite point on the cortical surface (the somatotopical 'point for point' projection mentioned above).

In primates these connections are particularly numerous in the system of the visual analyser and unite the zone of most acute vision in the retina (the field of the yellow spot) with the corresponding sector of the central visual field. There are data indicating that the number of these fibres passing mainly to the area of the occipital pole of the hemisphere constitutes more than half the number ascending from the subcortical relay-nucleus of the analyser (the lateral geniculate body) to the visual zone of the cortex.

In the ascending sequence of mammals a more and more detailed, progressive differentiation of the central sections of the analyser systems occurs on the somatotopical principle not only in the cortex but also in the subcortical impulse-switching stations. Thus rabbits still have no distinct topographical delimitation within the switching relay-nucleus of the thalamus of the recepts received from different parts of the body; but differentiation of a somatotopical type is already well marked in this nucleus in cats (Robiner, 1959). And it is even more distinctly marked in primates in connection with the considerably advanced structural and functional differentiation of the cortical zone of the analyser.

Apart from the primary (central) field of the cortical zone of each analyser there are secondary (peripheral) fields (see Plate V and Fig. 46, fields 18 and 19, 42 and 22, 1 and 2, 6 and 8), which are linked with the perceiving surface via a larger number of supplementary switches in the subcortical sectors of the analyser systems (see Plate VI and Fig. 53).

These cortical formations, as experiments and years of clinical observation have shown, perform more complexly mediated forms of reflection of the external world; and through them the functions of perception, imprinting, and correlation of more or less complex combinations of stimuli are performed. Thus when fields 18 and 19 are extirpated from a dog it has been observed that fine differentiation of visual stimuli is disrupted. The animal does not distinguish between objects similar in form, cannot, for example, distinguish between an octogon and a circle (Khananashvili,

1962). Other researchers have noted transitory desruption of visual acuity, perception of distance, and discrimination of the colour, shape and size of objects and of the direction of movement with similar lesions in the brains of monkeys (Koroleva, 1963). In man stimulation of fields 18 and 19 gives rise to more complicated visual perceptions than stimulation of field 17, in the form of imagined objects like coloured rings and balls, animal shapes, faces, etc. In particular, as the research of Luria and his colleagues has shown, the function of simultaneous perception and retention in consciousness of the many separate details of the object seen, from which its whole image is built up, must be assigned to the peripheral fields of the cortical zone of the visual analyser. As an example of the complex physiological syntheses performed in this zone we may take Ames' observations (1951, 1952). In his psychological tests the subject looked through an aperture in a box and saw a doll's chair suspended within it. As a matter of fact the different parts of the object were suspended separately in such a way that they gave the impression of a whole when viewed from a certain angle. The subject retained this illusory impression even when he was given the opportunity to confirm visually that the separate parts perceived as one whole object were spatially separated from one another.

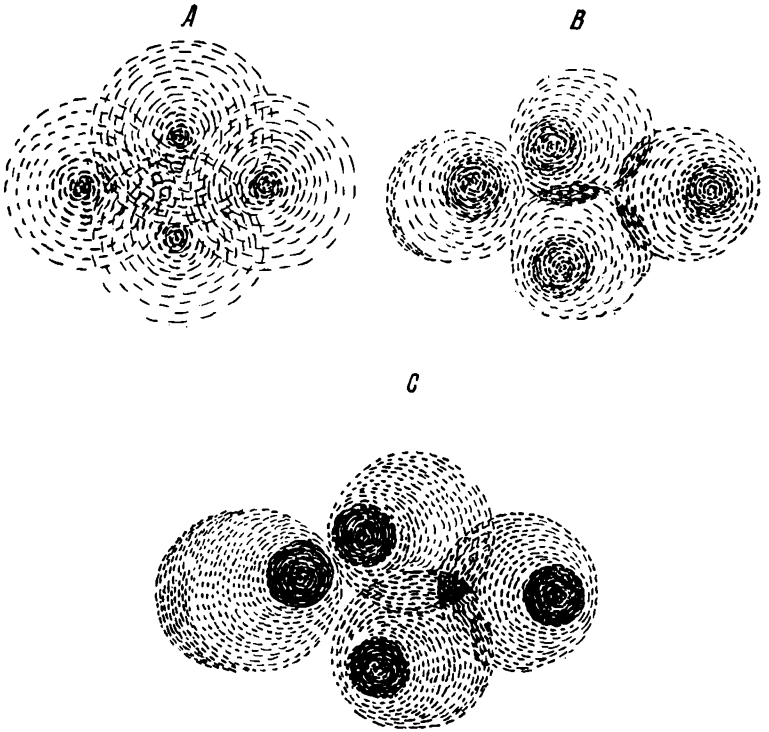
There are grounds for thinking that the topographical correlations between points on the perceptive and cortical surfaces are more complex in the secondary (peripheral) fields of cortical zones than in the primary (central) ones (see Plate V). In particular the principle of somatotopical 'point for point' projection does not apply in the secondary (peripheral) fields of the definite analyser systems, in contrast to the primary (central) fields. In all features of their structural organization the secondary fields are mainly adapted to providing a variety of functional connections between separate signal stimuli both within the limits of their own zone and in the complex of cortical zones belonging to other analysers.

In the course of evolution the topographical relations between the cortical representations of the various analyser systems have become more complicated in connection with the reconstruction of their functional interrelations brought about by the effect of an increasing complicated ex-

ternal environment on the organism. In addition to ever more detailed structural differentiation within the primary (central) and secondary (peripheral) fields of the cortical zones of the analysers (see Fig. 24 and Fig. 47), there is territorial expansion of the cortical zones of the various analysers with an ever greater mutual coming together of these zones and the formation of zones where they overlap. The last-named (which may also be called interanalyser zones) are quite fully represented in primates by anatomically specialized formations (see the fine dotted areas in Fig. 24). They embrace the upper (fields 5 and 7) and lower (fields 40 and 39) parietal regions, the middle temporal (field 21) and temporal-parietal-occipital (field 37) sub-regions (see also Plate V and Fig. 46). The same group may also include definite fields (9, 46, 10) of the frontal region (which it will be recalled constitutes nearly a quarter of the whole extent of the cerebral cortex in man) according to their functional importance and the place they occupy among the other fields.

The neurons of these cortical formations would seem to be linked with the sense organs and motor organs of the periphery in a most complex indirect way through a number of supplementary switches in the subcortical sections and the cortex (see Plate VI and Fig. 53). The physiological grounds for that conclusion are the fact that stimulation of the peripheral ends of the analyser systems, which brings about definite changes in the functional stages of the neurons of the primary (central) and secondary (peripheral) fields of the analyser zones, is not reflected in any marked way in the activity of the neuronal complexes making up the zones of overlapping.

The findings of comparative anatomy and clinical research provide indisputable evidence that the formations of the zones of overlapping are related to the most generalized forms of human perception and action, those most abstracted from concrete signal stimuli (the brain mechanisms of speech, labour processes, creative imagination, thinking, experience, and prediction). These zones seemingly represent the most important integral part of the apparatus of logical operations and of reflection of the most complex systems of relations between stimuli (orienters in the external world), being the material substratum of the processes of comparison and confrontation of objects according



F i g. 4 7. Diagrams representing consecutive stages in the progressive differentiation of the fields of the cortical zones and zones of overlapping of the cortical ends of the analyser systems in the course of mammalian evolution. The growing concentration of the central fields is shown (represented by the dark circles in diagram *C*), with their increasingly sharp delimitation from the peripheral fields of the cortical zones, and the progressive extension of the territory of the peripheral fields (depicted by the sparser fine broken lines in diagram *C*) with their mutual coming together and formation of zones of overlapping (depicted by the denser intersecting fine lines in diagram *C*). *A*, the lowest degree of differentiation, in which the cortical zones of the analysers are 'swamped' and are still weakly separated from one another; the diagram corresponds to the level of the neocortex in insectivores. *B*, a higher degree of differentiation, with marked demarcation of the cortical zones, and of their central fields (depicted by the heavier broken lines); zones of overlapping (represented by thicker intersecting lines) are still weakly expressed. The diagram corresponds to the level of development of the neocortex in rodents. *C*, a still higher level of differentiation with marked separation of groups of fields both within the cortical zones of the analysers and in the zones of overlapping; the diagram corresponds to the level of development in lower primates (after Poliakov, 1958).

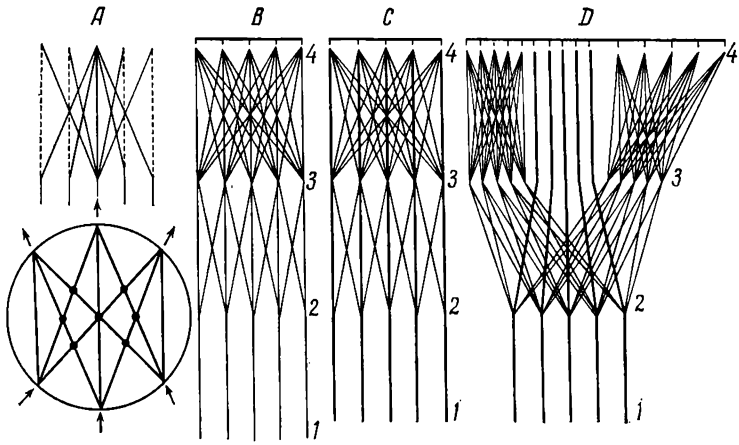
to the essential signs of likeness and difference (analysis and synthesis, and classification), judgment, deduction, etc.

The differences in functional significance briefly described above of the various fields of the cortical and overlapping zones of the analysers, which are brought about by the specialized features of the organization of their connections, can be illustrated in particular by Preobrazhenskaya's clinical findings and pathomorphological research (1952). Three clearly defined clinical syndromes were differentiated in cranial brain wounds according to the localization of the focus of damage in the visual and adjacent zones of the cortex. Damage to the central visual field and its connections was accompanied as a rule with more or less strongly marked disturbances of perception of visual stimulation while cases of considerable damage in this field resulted in cortical blindness. With lesions in the secondary (peripheral) fields of the cortical zone and their connections functional disturbances of visual recognition dominated the clinical picture. And when cortical fields of the lower parietal region and temporal-parietal-occipital sub-region bordering on the visual zone were involved, there were disturbances of the more complex forms of cortical integration resulting from the interaction of the visual analyser with other analysers. Disruption of constructive praxis, orientation in space, reading, and writing was observed.

Clinical data indicate that representation of the general body schema, and of the spatial relations of its various parts, are linked with the upper parietal region, which (as already said) may be included in the zones of overlapping of the cortical ends of the analysers. When this region is damaged disturbances of posture are observed, and disturbances of localization of the direction of movement and position of the various parts of the body.

4. General Scheme of Interconnections between the Various Switching Levels in the Analysers

In Section I of Chapter 3 we discussed a group of questions relating to the origin of the neuronal network. It was suggested that the principle of universal intersecting interconnections of all the elements involved in the transmission and transformation of nervous signalling was the founda-



F i g. 48. Schemes illustrating the progressive differentiation during mammalian phylogenesis of the basic structure or 'lattice' of interconnections of all levels of switches along an analyser system. *A* (top). Scheme showing the potential connections between a point at the lower level of switches and each point at a higher level (and the reverse). *A* (bottom). For comparison, scheme of the origin of an elementary neuronal network (see Fig. 26, *A*) oriented in the same direction. *B*. Scheme of the 'lattice' in mammals with weakly differentiated brain organization: *1*, receptor level; *2*, level of switches in the lower (axial) sections of the CNS (level of the lower sub-cortex); *3*, level of switches in the upper sub-cortex; *4*, switching level in the cerebral cortex represented in the other schemes. The 'lattice' of connections between all switching levels preserves a uniform character throughout its length. *C*. 'Lattice' scheme in mammals with higher differentiation of brain organization. Direct projections of definite points on the perceptive surface at definite points on the cortical surface are distinguished by the heavy lines within the 'network' across all levels of switches. *D*. Scheme depicting a further degree of progressive differentiation, with separation in the cortical zone of the analyser system of a central field in which direct 'point for point' projections are concentrated, and of peripheral fields in which predominantly indirect, intersecting connections between points on the perceptive and cortical surfaces are brought together.

tion of neuronal organization (see Fig. 27). Further, we noted that this principle, which reflects the commonest features of structure in the brain, also serves to explain the central switching apparatus in the analysers, the features of which have been reviewed in the preceding sections of this chapter. It is this idea of a 'lattice' type of interconnections that is, we suggest, the starting point for a ratio-

nal interpretation of the complex laws governing the structural differentiation of the cortical ends of the analyser systems and the character of their connections both between themselves and with their subcortical sections (formations of the upper and lower subcortex).

On that hypothesis geometrical diagrams can be constructed (Fig. 48) that reflect on the one hand the exact projection of definite points of the perceiving surface at corresponding points in the higher cerebral (cortical) end of an analyser system, and on the other hand the indirect, intersecting connections between any point perceiving stimulation and any point of the cortical end of the analyser system.* Thus the necessary conditions are created for the correlation of all possible combinations of stimuli that makes the analyser systems a universal instrument for adequate reflection (modelling) of changes in the external medium, with all-round evaluation of their signal significance for the organism. In addition, the diagrams of interconnections represented in Fig. 48 can contribute to understanding of the functional plasticity of the brain and of the interchangeability of its different parts (which finds clear expression in the phenomena of compensation and partial restoration of lost functions in focal lesions of the brain). It can be taken that they also hold interest for an explanation of the problems of reliability in a system as complex as the brain.

We consider the progressive differentiation of the analyser system during mammalian evolution as a process of gradual separation out from the originally fairly uniform 'lattice' of connections between various levels (see

* There is a striking resemblance between our scheme of a universal 'lattice' of interconnections underlying the organization of the whole system of neuronal switches in the brain and that worked out by Mikhalevich and Shor to illustrate the finding of the optimum solution of a problem by means of sequential analysis. That can be confirmed by comparing our Fig. 48 with the diagrams in Fig. 49 taken from Kondratov (1961). A similar example is the diagram of the principle of a 'perception' in Fig. 50 (after Kraizmer, 1962).

From these parallels it can be concluded that the most essential function performed by a complex analyser system and finding adequate expression in its structure is also the 'search', on the basis of an organization that provides a host of possible variants, for the optimum solution of its biological task by means of successive, stage-by-stage analysis and synthesis of the signals transmitted through its system of switches.

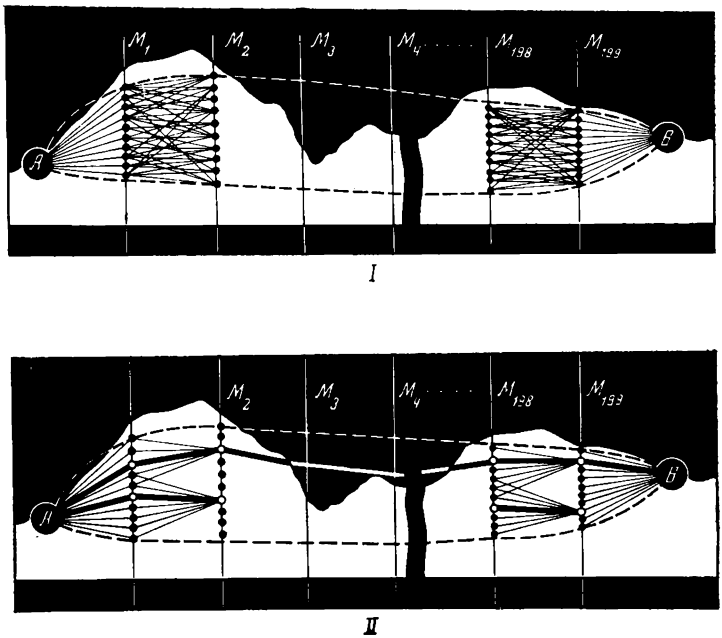
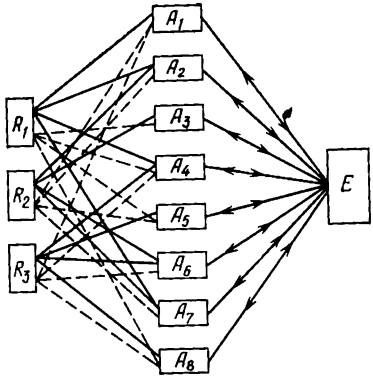


Fig. 49. *I*. Initial diagram depicting the search for the optimum variant of a railway line between points *A* and *B*. The number of possible variants rises in geometric proportion from sector to sector, reaching the astronomical figure of 10^{200}. *II*. Diagrams illustrating the computer solution of the problem utilizing sequential analysis. From the countless possible variants the machine selected the optimum ones, reducing the number until the separate sectors of track were joined together in a single optimum line for the future railway.

Fig. 48*B*), of various forms of organization of the switches linking its perceiving and cortical surfaces (see Fig. 48*C* and *D*). On the one hand there is a more and more powerful development and concentration in the core of the whole analyser system of switches and pathways through which the most direct ('point for point') projection of the perceptive periphery onto the central field of the cortical zone is achieved. On the other hand, parallel to and connected with that process, there is differentiation of the assemblages of switching neurons and conductors, which become more and more specialized along the line of establishing



F i g. 5 0. Diagram illustrating the operating principle of a perception, R_1, R_2, R_3, receptor cells; A_1,A_2, A_3, etc., association cells; E, effector cell (after Kraizmer, 1962)

indirect, intersecting links between points on the perceptive surface and points in the secondary (peripheral) fields of the cortical zone of the analyser.

This conception of brain structure agrees with the results obtained by experimental stimulation and extirpation of both the primary (central) and secondary (peripheral) fields of the cortical zones of the analysers. In particular it helps to explain the separate localization (organized on the principle of geometrical 'point for point' correspondence) of the projection in the central fields of the various groups of receptors and the existence of a complicated complexly grouped representation of the elements of the perceiving surface on the secondary (peripheral) fields.

The diagrams in Fig. 48 also enable us to explain a most essential differences between the construction of the cortical sections of the analyser systems and that of the analyser-coordination mechanism. In the higher vertebrates the cerebellum is the most highly developed formation of the analyser-coordination mechanism. Its cortex (which, from the features of its neuronal organization, can be considered the prototype of that of the cerebral hemispheres) differs characteristically from the cerebral cortex in having a uniform, homogeneous, 'monotonic' structure throughout its extent. In the cerebellum the cortical type has not, it would seem, reached the stage of morphological and physiological differentiation in which architectonic regions and fields differing in their structural and functional specialization are separated out. This constructional feature is

determined in turn by the fact that the cerebellar cortex, unlike the cerebral, works on one plane, as it were, i.e. performs a similar function of analysis and synthesis of one general complex of stimuli throughout its extent.

Correspondingly, the whole system of switches linking the cerebellar cortex with the receptor surfaces of the organism projected on it has already completed its development at the stage when its 'lattice' still preserves a uniform, relatively little differentiated, character (see Fig. 48*B*). Only with the development of analyser systems does the organization of interconnections between all levels of switches reach a higher degree of differentiation (see Fig. 48*C* and *D*). The further complication of their structure in comparison with that of the analyser-coordination mechanism was brought about by the following circumstance. Functional interactions between the analysers became more and more variegated as the evolution of mammals proceeded; as a result they became more and more closely interconnected both in their subcortical and, particularly, in their cortical sections.

The development and complication of the whole system of opposite projection links between the sense organs and the subcortical and cortical sections of the analyser systems was accompanied with a corresponding development and complication of two-way connections between the separate fields within the cortical zones and between the cortical zones of all the analysers represented in the cerebral hemispheres.

In the most differentiated cortical formations belonging to Filimonov's 'fully developed neocortex', a system of association connections (intercortical or cortico-cortical) is added to the systems both of projection (cortico-subcortical) and of intracortical connections (effected through neurons with short axons). Association connections become particularly well developed in the higher mammals (primates, and among the primates, man) (Plate VI and Fig. 53). It is interesting to note that the total number of projection and association fibres leaving the cortex would seem to exceed the number of fibres entering it by a more or less significant amount. According to Sholl (1956) the number of axons in a cubic millimetre of the visual cortex in a cat is around 100,000, of which three-quarters are efferent fibres and only one-quarter afferent.

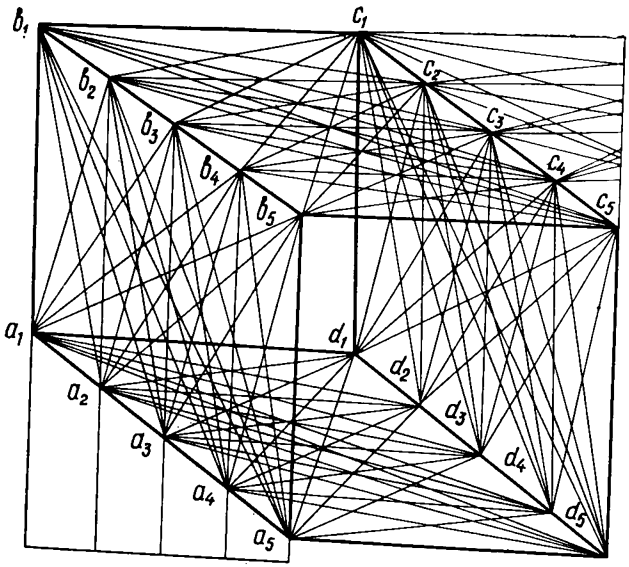


Fig. 51. Universal scheme of a 'lattice' of interconnections by means of which functional unity both of switching points in the subcortex (a_1—a_5) with the corresponding points in the cortex (b_1—b_2) (by way of projection connections) and of various groups of cortical neurons (the intersections of the 'lattice' links between b_1—b_5 and c_1—c_5) is achieved (by way of association connections). Attention is drawn to the fact that cortical points c_1—c_5 can be connected indirectly with subcortical points a_1—a_5 not only through the switches b_1—b_5 but also through supplementary switches in the subcortex d_1—d_5 (so-called association nuclei of the thalamus). The arrangement of switches in the cortex and subcortex presented in the diagram constitutes a single unit.

Various points on the cortex can interact closely by way of the system of association connections, and exchange stimulation. Thus the possibility of excitation being transmitted in the systems of the cutaneous and kinaesthetic analysers (and also in those of the visual and auditory analysers) from the central fields of their cortical zones to the secondary (peripheral) ones by the association connections linking them has been demonstrated by neuronographic techniques. Association connections have also been established by the same reasons between the different fields of the visual and auditory cortex. With the formation of

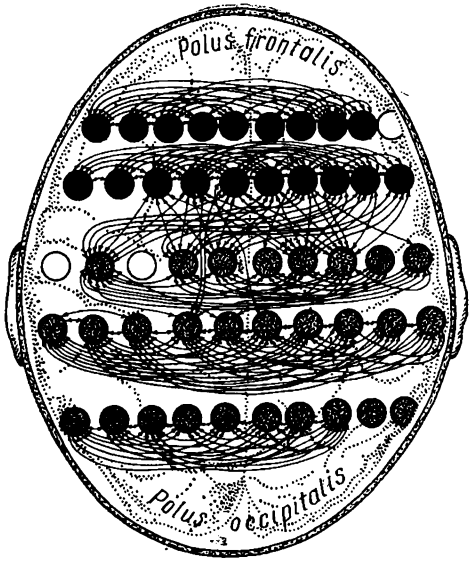


Fig. 52. Temporal correlation of points on the cerebral cortex during mental work (solution of a logical problem) (after Livanov, 1962)

this system of connections the anatomical and physiological conditions were created that ensure most complex functional interaction both within the cortical end of an analyser and between the cortical ends of different analysers.

It can be taken that the principle of a 'lattice' type of mutual intersection of pathways (Fig. 51) universal for the whole CNS underlies the system of both association and projection connections. We consider the results of Livanov's latest electrophysiological research (1962) to be confirmation of this. He investigated the problem of correlative analysis of biopotentials in the brain by simultaneous multichannel recording from many points on the cortex. As is shown in Fig. 52 the functional connections between correlated parts of the cortex are built up on the principle of mutual intersection, i.e. are of a 'lattice' type.

The division of the cortex into architectonic layers and sublayers is based on spatial delimitation of the complexes

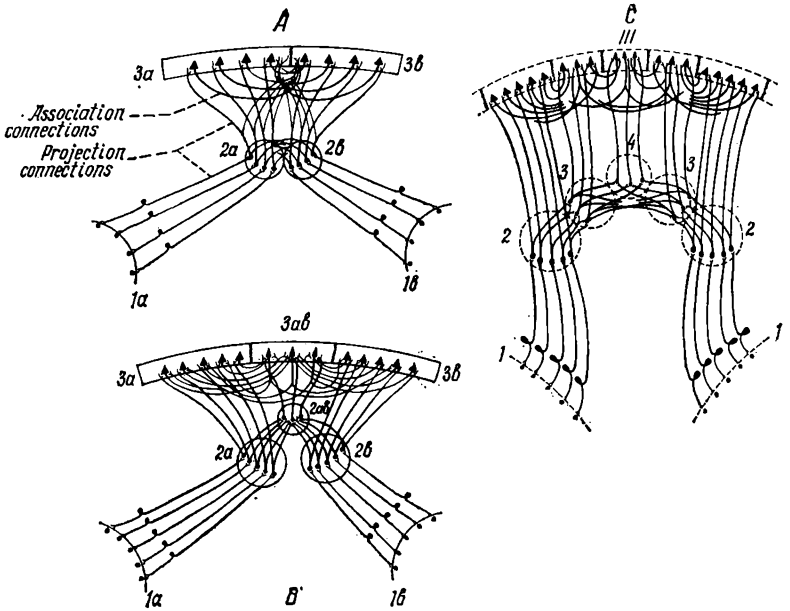


Fig. 53. Diagrams illustrating the successive complication of neuronal switches and connections in the analyser systems as a consequence of complication of their functional interaction in relation to the progressive structural differentiation of their cortical and subcortical switching instances. *A*. *1a*, *1b*, peripheral perceptive surfaces of the analyser systems; *2a*, *2b*, main switching nodes in the upper subcortex ('relay nuclei' of the thalamus) projecting in the cortical zones of the analyser systems (*3a*, *3b*). The beginning of the formation of supplementary projection and association connections is shown at the points where the cortical and subcortical sections of both analysers join and interact. *B*. The same, showing the differentiation of supplementary stations for switching impulses in the subcortical sections ('association nuclei' of the thalamus—*2ab*) and in the cortex (zone of overlapping of the cortical ends of the analysers —*3ab*). It can be seen that the main switching (relay) nuclei in the subcortical sections (*2a* and *2b*) are projected in the cortical zones of the analysers, while the supplementary ones (*2ab*) are projected in the zone of overlapping (*3ab*). *C*. Further lengthening of the chains of switches in the cortical and subcortical sections of both analysers is shown, with the corresponding complication of projection and association connections; *1*. peripheral perceptive surfaces; *2*, *3*, *4*, nodes of successive switches in the subcortical sections (thalamic nuclei and geniculate bodies); *I*, central (primary) fields; *II*, secondary (peripheral) fields; *III*, zone of overlapping. It can be seen that the main subcortical switching (relay) nuclei (*2*) are projected in the central fields, while the supplementary subcortical switching nuclei (*3*,*4*) are projected in the peripheral secondary fields and zone of overlapping (*A*—*C* after Poliakov, 1959-61).

of neurons and zones of synaptic junctions in its grey matter adapted for closing cortico-subcortical, intercortical, and intracortical connections (see Plate VI). The complication during evolution of the topographical relations between the complexes of neurons belonging to various systems of connections within the cortex itself, and with the subcortex, brought about the progressive differentiation of the cortex into different cyto-architectonic regions, sub-regions, fields, and sub-fields (Plate V and Fig. 46).

Comparative analysis of the material at our disposal on the complication of the CNS in ontogenesis and phylogenesis leads to the general conclusion that there is a definite correspondence in the development of all the systems of connections uniting the various sections of the cortex with one another and with subcortical formations.

In its most general features this regularity may be defined as the successive lengthening of the chains of neuronal switches in the cortex's systems both of projection and of association connections in the transition from primary (central) to secondary (peripheral) fields, and from them to the overlapping zones of the analysers (Fig. 53; see also Plate VI). Thus supplementary neuronal switches become separated in both the cortical and the subcortical sections of the analysers.

These supplementary groups of switching neurons prove to coincide first with the secondary (peripheral) fields and then to the overlapping zones (Fig. 53, *C*, *II* and *III*), which can be considered zones of blending and close functional interaction of the elements of various analyser functions. In the subcortical sections the anatomical expression of these processes is the formation of the 'association nuclei' of the thalamus, in which impulses from different analysers are brought together (Fig. 53, *C*, *3* and *4*). In certain sections of the thalamus there are groups of neurons that perform the role of an association collector of the general sensitivity of the body (somatic recepts). The most important association complex in the thalamus is the pulvinar, the sport where visual and auditory recepts converge. All these formations of the thalamus are united by numerous two-way (centripetal and centrifugal) connections with the zones where the cortical ends of the analysers overlap (the upper and lower parietal regions and the temporal-parietal-occipital sub-region).

Thus it can be concluded that neuronal organization undergoes most far-reaching transformation at places where qualitatively different streams of impulses join and interpenetrate. The overlapping zones in the cortical sections of the analyser systems and the subcortical sections linked with them, specialized as a result of these processes, are the most important constituents of the brain mechanism by means of which reactions to the most complex combinations of stimuli, and the relations between them, are effected.

The arrangement of interconnections described here is also the material foundation for various gradations of transition from concrete sensory perceptions and impressions to abstract, logical forms of cognizing reality and utilizing relations.

CONCLUSION

The perfection of the structure of the brain in the course of evolution as an organ of reflex activity is essentially manifested in the increasing the number of successive, superimposed levels of switching of nerve signals. As the organism's sphere of adaptive potentials broadened a specialization of ever more complexly organized morphological and physiological mechanisms took place in the originally weakly differentiated central nervous system that provided means for more and more branched chains of external and internal reactions directed to satisfying the organism's most vital requirements. These mechanisms include, in our conception, the coordination mechanism, the analyser-coordination mechanism, and the analyser systems.

The progressive development of reflex activity brought about by the influence of (dynamic) conditions of existence specific to self-organized biological systems of animal type has its source in the organism's capacity to make coordinated responses to stimuli, i.e. responses that are ordered both in space and time, and adaptive in character. The coordination mechanism, which is specialized earliest in the phylogenesis of both invertebrates and vertebrates, we consider to be the morphological and physiological basis of all vitally important auto-regulations performed within the organism and expressing itself in its reactions to external stimulation in the course of constant adaptation to changes in the surrounding medium.

In our view analysers take form in the evolution of the animal kingdom as brain mechanisms possessing many 'entries' and 'exits' to the periphery of the body supplementing the coordination mechanism. The fundamental biological significance of these central nervous formations is to carry

out afferent syntheses within the organism's sphere of recepts itself. As a result the necessary anatomical and physiological preconditions are created for realizing qualitatively higher forms of processing all the signals received by the central nervous system than those provided by the simple coordination mechanism. On that basis programmes of responsive reactions are elaborated that ensure mobile adaptation to rapidly and variously changing combinations of signal.

The lower stage of development of analysers, anatomically represented by the analyser-coordination mechanism, can be characterized as an arrangement for achieving functional unification of the organism's various auto-regulating adaptations as a whole. This form of central nervous integration, embracing whole complexes of auto-regulations belonging predominantly to the animal life of the organism, we designate as the function of auto-control.

A higher stage of development of analysers are the more complexly organized chains of neuronal switches, i.e. systems of analysers in the proper sense of the word. The higher (supra-axial) sections of the analyser systems formed in vertebrates by the end-brain are related to the most complexly integrated phenomena of reflex activity, both congenital and acquired during the individual's life, from which the organism's behaviour as a whole is built up. The chains of innate reactions, of the type of instincts, linked with the phylogenetically older cortical and subcortical formations, and brought about by the aggregate of the organism's biological requirements, we class together in the concept of auto-direction. The phylogenetically younger cortical and subcortical formations, with which are linked the processes of accumulating individual experience reproducing the most complex cerebral models of the environment, and elaborating corresponding programmes of behaviour, we look upon as the morphological and physiological basis of the function of direction in the full sense.

The stations for switching impulses located along the axial part of the central nervous system, and belonging to the analyser systems, are under the constant influence of opposite streams of impulses (centripetal and centrifugal) and have numerous collateral connections with the groups of neurons of the coordination and analyser-coordination mechanisms. On the basis of that arrangement, we

suggest, are performed the functions of regulation and control, which in our conception have important auxiliary significance for the functions of auto-direction and direction.

From the standpoint of evolution we look upon the origin and development of analysers as a further complication and qualitative transformation of fundamental features of neuronal organization that are already found in the coordination mechanism in a more elementary form. Analysers are built from the same basic types of neurons—efferent and internuncial (intermediate or intercalary) as the coordination mechanism. The complication of the general scheme of switches in the analysers, compared with the coordination mechanism, can be looked upon as a multiplication of the latter's elementary piece linked in parallel and series; each such elementary unit of the neuronal network is formed by a definite combination of interconnections between afferent fibres, and efferent and internuncial neurons.

The internuncial neurons in the analysers, apart from reticular elements typical of the coordination mechanism, are represented mainly of finer, more complexly differentiated elements—neurons with short axons that attain particularly significant development in the higher cerebral ends of the analyser systems. Coordination of the interactions between the separate groups of efferent neurons in the chains of switches along which signals specific to each analyser system are transmitted and processed is realized through active involvement of a similar type of neuron.

Neurons with short axons, together with the recurrent collaterals of the axons of efferent neurons, also play a very essential role in closing the circuits of circulating impulses in definite constellations of neurons located both in any one and in different levels of the central nervous system. Thanks to a corresponding organization of connections between afferent fibres and efferent and internuncial neurons optimum conditions are provided for fine discrimination and adequate reflection of separate signal stimuli, and their spatial and temporal complexes; a similar arrangement is also of essential importance to retain traces of excitation from stimuli operating earlier and to link them with current reactions. Neurons with short axons (stellate cells) are especially numerous in the cerebral cortex and differentiated in a variety of ways both in shape and in the features of their dendrites and axon branchings which

substantiates our conception of their importance in the cortical processes of analysis and synthesis of internal and external signals.

In the formations of the fully developed neocortex, which form the higher cerebral ends of the analysers in mammals, the organization of the different forms of interneuronal connections attains its greatest complication in comparison with the lower levels of the central nervous system. Apart from the terminal contacts of the axon branchings with the bodies of nerve cells and the initial sections of their dendrites, primarily adapted for the direct influencing of one neuron by another, we have also observed numerous contacts in these cortical formations of a tangential type established between the ramifications of axons and the appendages ('spines') on the dendrites of efferent neurons (pyramidal and fusiform cells). We would suggest that indirect influences are exerted on the functional state of an efferent neuron by many other neurons by way of these contacts. Their very considerable development in the cortex can be taken as morphological confirmation, from our point of view, of the high functional plasticity of cortical neurons.

The stellate cells with short axons (and also reticular neurons), unlike efferent neurons with long axons, are specialized by all the features of their fine structure and connections mainly for establishing terminal contacts with other neurons. These morphological facts accord with our modern conceptions of the role of internuncial neurons in the finest processes of differentiation and integration of the excitation reaching the cortex of the brain and circulating in its grey matter.

Our hypothesis of the origin of natural network of neurons enables us to develop a single, synthetic picture of the character of the progressive complication of neuronal organization in the course of evolution. On it we have based a scheme of lattice-like intersecting connections between neurons of the different levels of switching of impulses along analysers, from their peripheral to their higher cortical ends. A similar arrangement permits any point on a stimulus perceiving surface of an analyser at the periphery of the body to be linked in principle with any point in its cortical zone through a number of intermediate switches in the lower and upper subcortex.

Utilizing that conception, we can represent the complication of the structure of analyser systems in the course of evolutionary progress as the gradual differentiation, from an elementary, uniform, 'diffuse' 'lattice' of connections, of chains of neuronal switches more and more finely specialized for transmitting qualitatively different streams of impulses. In that way there came about in the stem part of an analyzer system a differentiation of tracts adapted to the shortest and most direct projection, involving a fairly minimal number of intermediate switches, from the periphery to the central field of its cortical zone. By means of such projections, organized on the somatotopical principle, a highly concentrated flow of 'specific' signals of corresponding modality is transmitted; the capacity of the analyser system for high 'resolution' is thus ensured, enabling fine differentiation (discrimination) of the separate properties of signal stimuli to be made.

In the course of the complication of analytical and synthetic activity in the analyser systems longer chains of neurons with a greater number of intermediate switches also became differentiated (an addition to the relatively short and direct pathways), uniting elements of the perceiving surfaces of the body with the secondary (peripheral) fields of their cortical zones. This part of their structure enables more complexly mediated interactions to be effected between groups of receptors and corresponding complexes of cortical neurons; signals despatched from one and the same point on the perceptive surface can thus reach various points of the cortex, while signals from various points on the perceptive surface converge on one and the same point in the cortex. Thanks to that organization of connections the anatomical and physiological prerequisites for a variety of forms of integration of finely discriminated signal stimuli are created.

The anatomical expression of the increasingly complicated functional relations between the analyser systems in a number of mammals is the formation, in addition to further structural differentiation of the cortical zones of analysers into primary (central) and secondary (peripheral) fields, of zones of overlapping of their cortical ends.

In the zones of overlapping, in contrast to the cortical zones (which can be characterized as areas of concentration of elements of a definite modality specific to a given analy-

ser), elements of various analysers located close beside one another are brought together. These 'interanalyser' zones, represented by fields of the upper and lower parietal regions, the temporal-parietal-occipital sub-region, and the frontal region, attain their highest degree of development in primates, and especially in man. They are related to the most generalized forms of analytical and synthetic activity which have been built up from the complex interaction of elements of the various analyser functions. In the structural organization of the brain these complex processes find reflection in the considerable development in primates of the association connections of the cortex that unite the cortical zones of the various analysers between themselves and with the 'interanalyser' zones of overlapping.

The progressive differentiation of the cortical zones into primary (central) and secondary (peripheral) fields, and the simultaneous rise of separate zones of overlapping of the analysers in the cerebral cortex are also accompanied with a corresponding reorganization of the neuronal switches in the upper subcortex in the shape of formations of the so-called association nuclei of the thalamus that supplement its relay nuclei.

A definite correlation by degree of development can be established between all the systems of connections uniting the various sectors of the cortex and linking them with the subcortical formations. This law can be formulated as the successive lengthening of the chains of neuronal switches in the systems of both the projection and association connections of the cortex with a transition from the primary (central) to the secondary (peripheral) fields of the cortical zones of the analyser systems, and from them to the zones of overlapping.

To sum up, it can be said that the material so far accumulated on the architectonics, neuronal structure, and connections of the central nervous system already enables us to make certain generalizations about the structural organization of the various reflex mechanisms of differing functional significance. Comparative analysis of the origin, development, and complication during evolution of these mechanisms brings us nearer to a solution of the cardinal problem posed by Pavlov, of what parts constitute the analysers and how those parts interact on one another.

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